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FERNS AND FERN ALLIES
OF GUATEMALA

PART III
MARSILEACEAE, SALVINIACEAE,
AND THE FERN ALLIES
(INCLUDING A COMPREHENSIVE INDEX
TO PARTS I, II, AND III)

ROBERT G. STOLZE

The Genus *Lycopodium* by:
BENJAMIN ØLLGAARD

The Genus *Isoetes* with:
R. JAMES HICKEY

August 31, 1983

Publication 1349

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ROBERT G. STOLZE
*Custodian, Pteridophyte Herbarium
Field Museum of Natural History*

The Genus *Lycopodium* by:
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FERNS AND FERN ALLIES OF GUATEMALA

This is the final fascicle of a three-part series concerning the pteridophyte flora of Guatemala. "Part I: Ophioglossaceae through Cyatheaceae" was published in *Fieldiana: Botany*, Volume 39, 1976, and "Part II: Polypodiaceae" (*sensu lato*) was printed in *Fieldiana: Botany*, New Series, No. 6, 1981. A comprehensive index to the entire pteridophyte flora can be found near the end of the present publication. A key to the families of Guatemalan ferns and "fern allies" was published in Part I of the series.

A key to each genus of the "water ferns" and "fern allies" is given in the following pages. Descriptions and discussions of the genera are provided, as well as keys to the species, which are then arranged in alphabetical order. At least one illustration is provided for each genus treated, to point out the important or diagnostic features of genera and species. *Lycopodium* has been divided into three subgenera by its author, Benjamin Øllgaard, and a key to the subgenera is provided.

The Central American republic of Guatemala is bordered on the north and west by Mexico, on the east by Honduras and El Salvador, on the south by the Pacific Ocean, and on the northeast by the Caribbean Sea. The country encompasses an area of nearly 110,000 sq km and is divided into three rather distinct zones. A relatively narrow band of lowlands borders the southern (Pacific) side, which is devoted primarily to farming (cotton and sugarcane) and cattle. The central highlands form a broad, east-west band of hills and high mountains which reach to an altitude of 4,200 m (Volcán Tajumulco). These highlands support the bulk of the country's population, extensive corn fields and coffee plantations, and an exceedingly rich natural vegetation. The northern half of the country is thinly populated and consists mainly of grasslands and lowland tropical rainforests.

To illustrate the richness of the pteridophyte flora of Guatemala, it should be pointed out that this country is less than 1% the size of the United States, yet it supports nearly three times the number of species of ferns and fern allies as does its big northern neighbor. Within this three-part flora are to be found a total of 101 genera and 652 species of pteridophytes. Included in the treatment are species found in British Honduras, a British dependency, now under self-rule, which is claimed by Guatemala and whose borders are also currently under dispute. Although the name was changed to Belize in 1973, "British Honduras" had been used throughout the "Flora of Guatemala" and is thus used in this pteridophyte flora as well, for the purposes of continuity. But whatever social and political problems accrue from international disagreements and border changes, the flora of this area is essentially Guatemalan, being virtually an extension of that of the northern lowland tropical rainforests.

A list of the genera and number of species of pteridophytes to be found in the Flora is presented here, arranged alphabetically according to family and genus:

FERNS**CYATHEACEAE**

<i>Alsophila</i>	1
<i>Cnemidaria</i>	1
<i>Cyathea</i>	3
<i>Lophosoria</i>	1
<i>Metaxya</i>	1
<i>Nephelea</i>	2
<i>Sphaeropteris</i>	2
<i>Trichipteris</i>	8

DICKSONIACEAE

<i>Cibotium</i>	1
<i>Culcita</i>	1
<i>Dicksonia</i>	1

GLEICHENIACEAE

<i>Dicranopteris</i>	2
<i>Gleichenia</i>	5

HYMENOPHYLLACEAE

<i>Hymenophyllum</i>	22
<i>Trichomanes</i>	24

MARATTIACEAE

<i>Danaea</i>	3
<i>Marattia</i>	4

MARSILEACEAE

<i>Marsilea</i>	2
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OPHIOGLOSSACEAE

<i>Botrychium</i>	3
<i>Ophioglossum</i>	6

OSMUNDACEAE

<i>Osumunda</i>	2
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PLAGIOGYRIACEAE

<i>Plagiogyria</i>	2
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POLYPODIACEAE

<i>Acrostichum</i>	2
<i>Adenoderris</i>	1
<i>Adiantum</i>	28
<i>Ananthacorus</i>	1
<i>Anetium</i>	1
<i>Anogramma</i>	1
<i>Antrophyum</i>	1
<i>Arachniodes</i>	1
<i>Asplenium</i>	40
<i>Athyrium</i>	2
<i>Blechnum</i>	12
<i>Bolbitis</i>	4
<i>Bommeria</i>	1
<i>Ceratopteris</i>	3
<i>Cheilanthes</i>	14
<i>Cochlidium</i>	2

<i>Ctenitis</i>	14
<i>Cyclopeltis</i>	1
<i>Cyrtomium</i>	4
<i>Cystopteris</i>	2
<i>Demmstaedtia</i>	6
<i>Dictyoxiphium</i>	1
<i>Didymochlaena</i>	1
<i>Diplazium</i>	17
<i>Doryopteris</i>	2
<i>Dryopteris</i>	6
<i>Elaphoglossum</i>	38
<i>Eriosorus</i>	3
<i>Grammitis</i>	26
<i>Gymnopteris</i>	2
<i>Hecistopteris</i>	1
<i>Hemidictyum</i>	1
<i>Hemionitis</i>	2
<i>Histiopteris</i>	1
<i>Hypolepis</i>	2
<i>Jamesonia</i>	1
<i>Lastreopsis</i>	2
<i>Lindsaea</i>	7
<i>Llavea</i>	1
<i>Lomariopsis</i>	4
<i>Lonchitis</i>	1
<i>Loxogramme</i>	1
<i>Maxonia</i>	1
<i>Mildella</i>	1
<i>Nephrolepis</i>	6
<i>Notholaena</i>	9
<i>Oleandra</i>	2
<i>Onocleopsis</i>	1
<i>Paltonium</i>	1
<i>Pellaea</i>	7
<i>Peltapteris</i>	1
<i>Pityrogramma</i>	5
<i>Plecosorus</i>	1
<i>Pleuroderris</i>	1
<i>Polybotrya</i>	5
<i>Polypodium</i>	69
<i>Polystichum</i>	12
<i>Polytaenium</i>	3
<i>Pteridium</i>	1
<i>Pteris</i>	14
<i>Saccoloma</i>	2
<i>Schaffneria</i>	1
<i>Stigmatopteris</i>	2
<i>Tectaria</i>	6
<i>Thelypteris</i>	61

<i>Vittaria</i>	3	FERN ALLIES	
<i>Woodsia</i>	1	EQUISETACEAE	
<i>Woodwardia</i>	1	<i>Equisetum</i>	3
SALVINIACEAE		ISOETACEAE	
<i>Azolla</i>	2	<i>Isoetes</i>	3
<i>Salvinia</i>	2	LYCOPODIACEAE	
SCHIZAEACEAE		<i>Lycopodium</i>	24
<i>Actinostachys</i>	1	PSILOTACEAE	
<i>Anemia</i>	10	<i>Psilotum</i>	2
<i>Lygodium</i>	3	SELAGINELLACEAE	
<i>Schizaea</i>	1	<i>Selaginella</i>	26

All abbreviations of periodical publications follow the system of *Botanico-Periodico-Huntianum*, Hunt Botanical Library, Pittsburgh, Pennsylvania, 1978.

ACKNOWLEDGMENTS

My deepest expression of gratitude is tendered to Benjamin Øllgaard of the Botanical Institute of Aarhus University in Denmark for contributing the treatment of *Lycopodium*, and to R. James Hickey of the University of Connecticut for collaborating with me on the treatment of *Isoetes* (Jim's was the "lion's share" of the work). Both of these genera are extremely difficult, and I was fortunate to enlist the aid of the two men who are presently engaged in revisions of their respective genera.

Although research has been based chiefly on the excellent collections of the John G. Searle Herbarium at Field Museum, nearly 1,000 additional specimens have been borrowed from the following institutions: U.S. National Herbarium, Washington, D.C., Gray Herbarium, Cambridge, Massachusetts; New York Botanical Garden, Bronx, New York; Museo de Historia Natural, Guatemala City. I would like to express my gratitude to the curators of these herbaria for loaning their specimens for study.

If a "picture is worth a thousand words," then a thousand thanks are due Zbigniew Jastrzebski, not only for his excellent drawings, but also for his patience, cooperation, and understanding.

Nearly nine years ago, Dr. Louis O. Williams, Curator Emeritus (then chairman of the Botany Department) at Field Museum, urged me to do a treatment of the pteridophytes, to supplement the work nearly completed on the monumental "Flora of Guatemala." Now that my task is finished, I look back with deep appreciation to the man who was the catalyst for this entire pteridophyte flora. I thank him warmly for his confidence, his counsel, and his friendship.

Although there has been no direct financial support for this final part of the "Ferns and Fern Allies of Guatemala," I must acknowledge the continued help given by the National Science Foundation (NSF) over a period of many years. This assistance supported research and fieldwork and, eventually, much of the publication costs, both for the "Flora of Guatemala" and for Parts I and II of the "Ferns and Fern Allies of Guatemala." Therefore, indirectly, the present volume would have been difficult, if not impossible, to produce without the support of NSF.

MARSILEACEAE

REFERENCES: J. G. Baker, Handbook of the fern allies, London, 1887. C. F. Reed, Index Marsileata et Salviniata, Bol. Soc. Brot. II. 28: 5-61. 1954.

Plants small, heterosporous, aquatic or subaquatic, often subject to desiccation during dry seasons; rhizome branched, usually slender and creeping, variously pubescent; leaves circinate in veneration, crowded to approximate or remote, simple and filiform (in *Pilularia*) or long-petiolate and with either 2 or 4 apparently opposite leaflets; sporocarps hard, nutlike, borne on or at the bases of leaves, long-stalked or sessile; sori containing both microsporangia and megasporangia.

This is a small, but cosmopolitan, family which contains the three genera *Pilularia*, *Regnellidium*, and *Marsilea*. Only the last is represented in Guatemala.

MARSILEA Linnaeus

REFERENCE: W. R. Maxon, Scientific survey of Porto Rico and the Virgin Islands, 6: 373-521. 1926, New York.

Plants rooted in mud, with their leaves erect or floating in water; leaf with a long and slender, sparsely pubescent or glabrate petiole which bears at its apex a cruciform lamina, this consisting of 4 flabelliform leaflets, thus resembling a 4-leaved clover; leaflets sessile, narrowly cuneiform to obovate-flabellate, glabrate to densely pubescent, with veins branching freely from the base, anastomosing, at least, toward the distal edge of the leaflet; sporocarp moderately to densely pilose, subglobose to oblong-ovoid, short- or long-stalked, borne singly or in 2s and 3s or in clusters, spreading horizontally or deflexed along the stalk, the stalk often terminating in a sharp tooth or low knob, and often another tooth or low projection present along the ridge (raphe) and adjacent to the end of the stalk; sori imbedded in gelatinous tissue within the 2 valves of the sporocarp, emerging at "germination" as a vermiform mass.

The genus is sorely in need of revision. Collectors, especially in the neotropics, seem either to pass by these plants, or to be unsuccessful in obtaining fertile material. While characteristics of the sporocarp are usually sufficient to ensure accurate identification in most species, features of petiole, lamina, type of pubescence, etc., are often woefully inadequate.

Marsilea contains 60 to 70 species scattered throughout the world, with the largest concentrations occurring in temperate regions of the eastern hemisphere. Only two species are found in Guatemala, with one other (*M. polycarpa*) perhaps to be expected here (see "Excluded Species").

- a. Leaflets (at least some mature ones) reddish striped between the veins on the abaxial side; sporocarps borne in dense clusters on a short stalk. *M. mexicana*.
- a. Leaflets lacking reddish stripes; sporocarps borne singly on a rather prominent stalk (stalk 1-2 times as long as sporocarp). *M. berteroi*.

Marsilea berteroi A. Br., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1870: 747. 1871. *Yerba de pulga* (fide Standley, Huehuetenango).

In swamps, wet meadows, roadside ditches, 1,800-1,900 m; Huehuetenango; Santa Rosa. Honduras; Puerto Rico; Hispaniola.

Rhizome creeping, sparsely provided with light brown, elongated, pluricellular trichomes, or glabrate; leaves crowded to approximate on the rhizome, 5-12 cm long, with wiry, suberect, petioles bearing flat, whitish to tawny trichomes 0.2-0.4 mm long scattered throughout (especially near the apex), or glabrate; leaflets 0.6-2 cm long, obovate-flabellate, the lateral edges straight to slightly concave, sparsely to moderately pubescent at maturity (as on the petiole) or glabrate, the constricted base stramineous to brownish

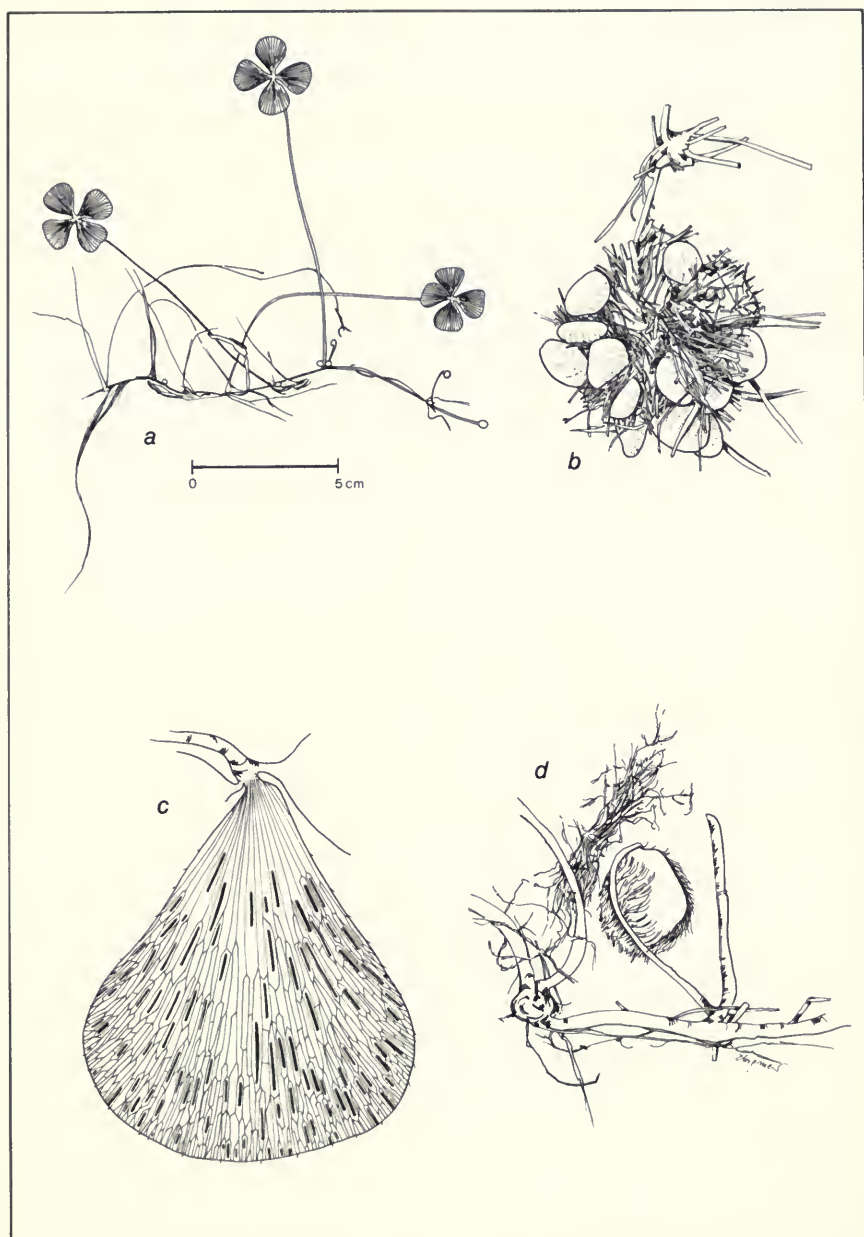


FIG. 1. *Marsilea*. a—c, *M. mexicana*: a, habit, $\times \frac{1}{2}$; b, cluster of sporocarps, $\times 3$; c, portion of leaflet, with red stripes between veins, $\times 6$; d, *M. berteroi*, part of rhizome with sporocarp, $\times 3$ (some trichomes removed).

and somewhat cartilaginous, veins prominent, free in the proximal $\frac{1}{3}$ – $\frac{1}{2}$, rather frequently anastomosing distally; sporocarp commonly oblong-ovoid, spreading horizontally, or strongly deflexed along a stalk which is 1–2 times its length, the stalk often terminating in an obtuse knob at its point of attachment, and with another low, rounded projection present along the raphe and adjacent to the end of the stalk.

Features of the sporocarp are sufficient to separate this from *M. mexicana*, but with sterile material, the task may be much more difficult. See discussion of the latter for further details.

Marsilea mexicana A. Br., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1870: 747. 1871.

In ponds, shallow waters around lake shores, marshes, wet meadows and roadside ditches, 400–2,000 m; Chiquimula; Huehuetenango; Jutiapa; El Quiché. Mexico; Honduras.

Rhizome commonly wide-creeping, sparsely provided with whitish to brown, elongated pluricellular trichomes, or glabrate; leaves approximate to subdistant, or remote, 4–25 (–30) cm long, with slender, suberect petioles bearing flat, whitish trichomes 0.2–0.4 mm long scattered throughout or glabrate; leaflets 0.5–3 cm long, obovate-flabellate, the lateral edges straight to slightly concave, sparsely pubescent at maturity (as on the petiole) or glabrate, reddish (or orange-) striped between the main veins on the abaxial side, the constricted base yellowish to brown and somewhat cartilaginous, the veins well to moderately defined (sometimes obscure), free in the proximal $\frac{1}{3}$ or $\frac{1}{2}$, rather freely anastomosing distally; sporocarps borne in dense clusters on short stalks from the rhizome, along with short, terete, rootlike structures, ovoid to subglobose, strongly deflexed along a stalk about its same length, the stalk often terminating in an obtuse knob at its point of attachment, and with another low, rounded projection present along the raphe and adjacent to the end of the stalk.

With sterile material, it is often difficult to distinguish this from *M. berteroi* and other species from the neotropics. The major diagnostic vegetative feature is the reddish or orange stripes (glands?) which occur between and parallel with the main veins on the abaxial side of leaflets. However, these are generally found only when laminae are mature and, frequently, not even then. Thus, one may need to examine nearly all the mature leaves on a specimen before detecting the stripes. On the other hand, some plants have been observed with nearly all the leaves, mature and immature, clearly red-striped. Revisionary work in the future might even reveal that none of the leaflets in a given specimen of *M. mexicana* bear the stripes. Therefore, this character would turn out to be less efficacious than it now appears. Unfortunately, problems of determination are additionally compounded by the paucity of fertile collections. Of the many specimens examined during the course of this study, only one in 20 bore sporocarps.

EXCLUDED SPECIES

Marsilea polycarpa Hook. & Grev., Icones Filicum t. 160. 1829. *M. brasiliensis* Mart., Icones Plantarum Cryptogamicarum 122: t. 73. 1834.

Maxon (1926) reported this species from the Greater Antilles, "Mexico southward sparingly to Brazil"; Tahiti.

Fertile plants of *M. polycarpa* cannot be confused with any other species. Numerous sporocarps are borne in a long line along the petiole, whereas in other species they occur singly, or in twos and threes, or in rather dense clusters. Unfortunately, problems of identifying infertile material are as problematical in *M. polycarpa* as in

many other species. Hence, it is quite possible that this is represented among the several sterile collections I have examined from Guatemala and which I have been unable to identify with confidence. Of these, none have reddish striped leaflets, so one could assume these specimens are not *M. mexicana*. It is likely they are *M. berteroi*, but leaflets of the latter are scarcely distinguishable from those of *M. polycarpa*, and since this species has been found in Mexico and Honduras, it might be expected to occur in Guatemala as well.

SALVINIACEAE

REFERENCE: C. F. Reed, Index Marsileata et Salvineata, Bol. Soc. Brot. II. 28: 5–61. 1954.

Plants heterosporous, small to minute, aquatic, free-floating or occasionally resting in mud; rhizome branched, horizontal, bearing simple roots or (in *Salvinia*) none at all and the submerged leaves serving the root function; leaves straight in veneration, either floating or submerged, entire to (in *Azolla*) 2-lobed, or the submerged, rootlike leaf in *Salvinia* highly branched; sporocarps borne at the bases of leaves or along their margins, protected by a thin-walled indusium containing either megasporangia or microsporangia; megasporangia each containing a single megaspore; microsporangia each bearing numerous microspores.

This is a small family with widely distributed species. As recognized here, it contains the two genera, *Azolla* and *Salvinia*, but a number of workers now prefer to consider each genus in a separate family of its own.

- a. Leaves distichous, 2-lobed, 1 lobe floating, the other submerged, the largest of the lobes 0.4–1.2 mm long; true roots present. *Azolla*.
- a. Leaves in whorls of 3, 2 floating and entire, 1 submerged and highly divided, the largest of the floating leaves 0.6–2.5 cm long; roots absent, but the submerged leaves serving the root function. *Salvinia*.

AZOLLA Lamarck

REFERENCES: H. K. Svenson, The New World species of *Azolla*, Amer. Fern J. 34: 69–84. 1944. A. H. Pieterse, L. de Lange, and J. P. Van Vliet, A comparative study of *Azolla* in the Netherlands, Acta Bot. Neerl. 26: 433–451. 1977.

Plants with rootlets trailing, 0.5–5 (–6) cm long, dorsiventral, pinnately to subdichotomously branching, often forming dense mats on the water; leaves reddish to greenish, distichous, approximate or imbricate, 2-lobed, the lobes opposed, the upper lobe floating, the largest of these 0.4–1.8 mm long, the lower lobe submerged and usually larger than the upper; sporocarps commonly in pairs in the axils of older leaves, protected by a membranaceous indusium; megasporangium ellipsoid to acorn-shaped, consisting of a single large megaspore with its appendages, ca. 0.5 mm long, somewhat pointed and usually castaneous on the distal end, rounded and greenish proximally; microsporocarp globose, often more than 1 mm in diameter, bearing numerous long-pedicellate microsporangia, each of which contains (3–) 4–6 (–10) spore-masses (massulae) bound together by a thin coating of hardened protoplasmic matter; massulae armed with glochidiate trichomes, each massula consisting of numerous microspores; microspores trilete, tetrahedral, with perine.

Species of *Azolla* are easily confused, since vegetative characters have thus far been of little help, and about 70% of most collections are sterile. Of the fertile collections, about half will be found to lack either megasporangia or microsporangia. Furthermore, it is necessary to use a compound microscope for determining fertile material with certainty.

There are six to seven species widely distributed throughout the world, four of

them in the New World. Their reddish or green leaves, in the habit of duckweed (*Lemna*), may form dense floating masses, frequently coating the entire surface of smaller bodies of water. Plants are supported on the water by the lower leaf lobes. In younger growth, both upper and lower lobes are appressed and usually strongly imbricate, but in age, the upper lobes often spread upward. At the base of leaves and at the growing point of the stem, the filaments of the blue-green alga, *Anabaena*, frequently can be observed.

In spite of Svenson's fine work (1944) on the New World species of *Azolla*, a number of problems remain unresolved in the taxonomy of this small and difficult genus. Svenson's most valuable characters for diagnosis are the septate vs. non-septate glochidiate trichomes on the massulae, and the type of surface sculpturing on the megaspore. However, occasional specimens are found where trichomes are both septate and nonseptate, and megaspores have yet to be found in *A. caroliniana* Willd. Some use of vegetative characters has been made, such as pinnate vs. subdichotomous branching, shape and size of leaf lobes, and types of trichomes and/or papillae on leaf surface, but none have yet proved consistent, nor been successfully correlated with sporangial features. A thorough monographic study is now needed, including a close examination of live plants, coupled with the collection of better and fertile specimens, and more precise field observations.

Two species, *A. filiculoides* and *A. microphylla*, are definitely known to occur in Guatemala. *Azolla mexicana* perhaps may be expected here, and indeed some of the sterile collections I have examined could be this species. However, sterile material cannot be identified with certainty. See discussion of *A. caroliniana* and *A. mexicana* under "Dubious and Excluded Species" below.

- a. Massulae provided with nonseptate glochidia; surface of megaspores proximally provided with low, broadly rounded protuberances; most upper leaf lobes imbricate and moderately to strongly appressed. *A. filiculoides*.
- a. Massulae provided with several- to many-septate glochidia; surface of megaspores smooth; most upper leaf lobes spreading, not or scarcely imbricate. . . *A. microphylla*.

***Azolla filiculoides* Lam., Encyclopédie Méthodique Botanique 1: 343. 1783.**

In lakes, ponds, wet ditches, quiet edges of streams, and occasionally in wet or marshy meadows, 600–1,900 m; Escuintla; Huehuetenango; Jalapa; Sololá (sterile collections, probably *A. filiculoides*, also found in Guatemala and Sacatepéquez). Mexico; Honduras. Other specimens, also determined by H. K. Svenson (Amer. Fern J. 34: 79. 1944), are said to have been found from Alaska, California, and Arizona and from Colombia to Chile, as well as a single collection from Hawaii. Some Andean plants were found growing in "a rather dry substratum. . . in thick masses."

Plants (0.5–) 0.8–5 cm long, pinnately to subdichotomously branching; upper leaf lobes mostly imbricate and moderately to strongly appressed, elliptic, oblong, spatulate to ovate, obtuse to subacute, with a narrow to (usually) broad, pale margin, papillose or scurfy-papillose on the surface, larger ones 0.5–1.2 mm long, the lower lobes about the same size to substantially larger; surface of megaspore, at the proximal end, provided with low, broadly rounded protuberances; microsporangia containing (3–) 4–6 (–8) massulae, the latter armed with nonseptate glochidia.

Various workers have claimed that vegetative characters may be used to separate species of *Azolla*. Svenson (1944) claimed that "When a series of fruiting plants has been recognized, the elongate-frondose character and curled leaves of well-

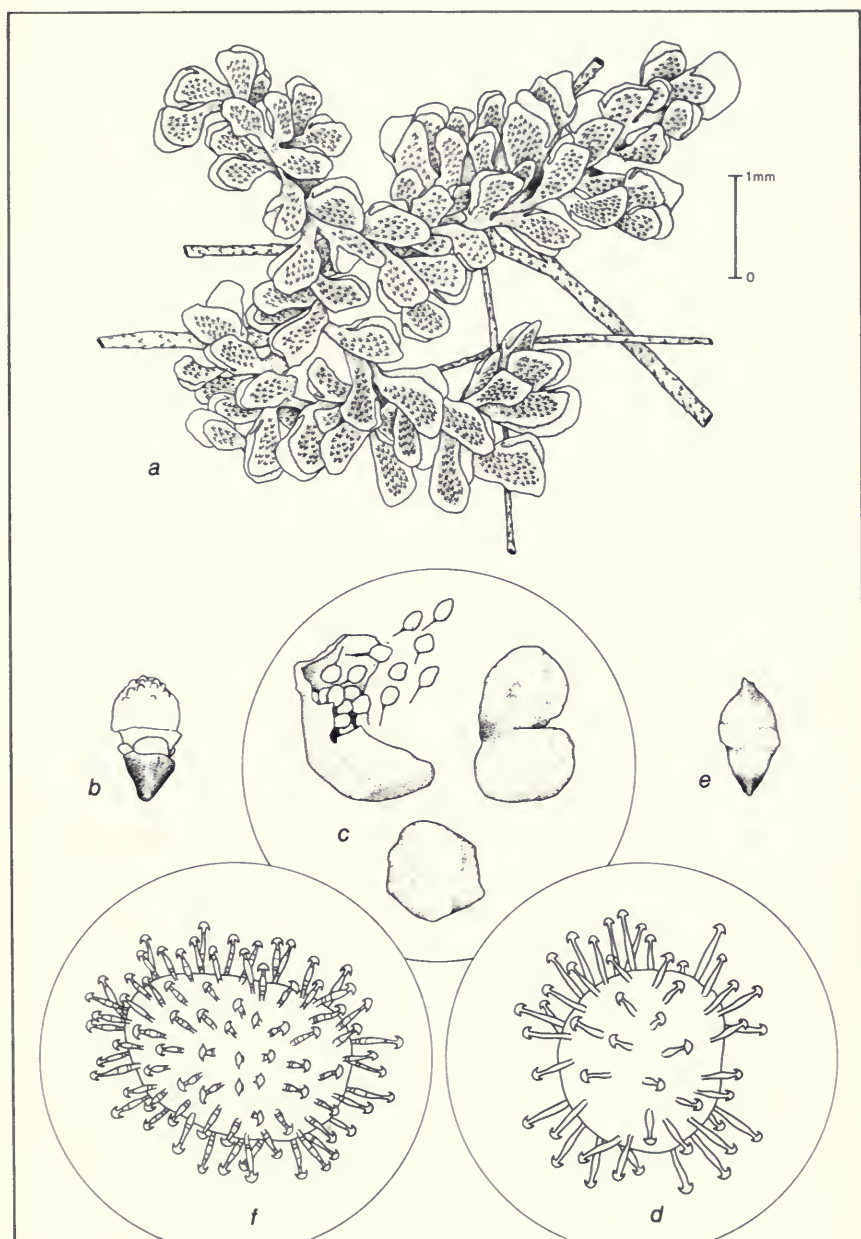


FIG. 2. *Azolla*. a–d, *A. filiculoides*: a, habit, $\times 18$; b, megasporangium, $\times 33$; c, sporocarp indusia with microsporangia, $\times 15$; d, massula with nonseptate, glochidiate trichomes, $\times 240$. e–f, *A. microphylla*: e, megasporangium, $\times 33$; f, massula with septate, glochidiate trichomes, $\times 240$.

developed *A. filiculoides* can be perceived at a glance." Leaf size and pinnately vs. dichotomous branching are other characters thus suggested. It is true that plants and leaves of *A. filiculoides* are frequently larger than (for instance) *A. microphylla*, but the measurements overlap so often that this is not a consistent guide. In the above key, I have included the subsidiary feature of spreading vs. appressed and imbricate leaf lobes, but this must be used with caution. If there are any vegetative characters that are consistently diagnostic, I have failed to perceive them.

***Azolla microphylla* Kaulf., Enumeratio Filicum 273. 1824.**

Only two Guatemalan collections (*Steyermark 31827 & 31832a*) have been positively identified: floating on surface, around margins of Lago Güija, southeast of Asunción Mita, Dept. Jutiapa, altitude 470–500 m. Other infertile collections which are probably *A. microphylla* have been seen, from Chimaltenango, Huehuetenango and El Quiché, 1,500–2,200 m, floating on the surface of ponds. Other fertile collections have been noted from Honduras, El Salvador, and Nicaragua, 100–900 m, in ditches, ponds, lakes, and quiet pools of rivers. In addition, Svenson (1944) has cited fertile material from the Dominican Republic, the Guianas, Brazil, Bolivia, and the Galapagos Islands.

Plants 0.5–1.2 (–1.7) cm long, pinnately to subdichotomously branching; upper leaf lobes scarcely or not at all imbricate, spreading (although newer ones often appressed and imbricate), elliptic, oblong or spatulate, obtuse or rarely subacute, with a narrow to rather broad, pale margin, papillose on the surface, larger ones 0.4–0.7 (–0.9) mm. long, the lower ones subequal or (more often) larger; surface of megaspore smooth; microsporangia containing 3–4 (–5) massulae, the latter armed with several- to many-septate glochidia.

As in the case of *A. filiculoides*, vegetative characters cannot be relied upon consistently, but one feature can be used with some confidence. The upper leaf lobes in *A. microphylla* are commonly obtuse, although here and there are some which might be described as subacute. In *A. filiculoides*, acute or subacute upper leaf lobes are frequent, although a number of obtuse lobes can always be found. See discussion of *A. filiculoides* for further comparison of diagnostic features.

DUBIOUS OR EXCLUDED SPECIES

***Azolla caroliniana* Willd., in L., Species Plantarum, ed. 4, 5: 541. 1810.**

Specimens of all American species of *Azolla* may be found in most herbaria mistakenly determined as *A. caroliniana*. This name has been a "catch-all" for most sterile material, or for specimens filed by curators unfamiliar with the taxonomic problems in the genus. The principal difficulty is that rarely have fertile specimens ever been collected, and these only with microsporangia. Glochidia are non-septate, so fertile material can be confused only with *A. filiculoides*. The latter is generally a much larger plant, mostly more than 1 cm long, with upper leaf lobes to 1.8 cm long. Plants of *A. caroliniana* are commonly 0.5 cm long, with upper leaf lobes about 0.5 mm long. With sterile material, the problem is complex, for other vegetative characters are of little diagnostic help. Svenson (1944) maintains that *A. caroliniana* is confined to eastern United States, with perhaps a few collections noted from the Greater Antilles.

***Azolla mexicana* Presl, Abh. Königl. Böhm. Ges. Wiss. V. 3: 150. 1845. *A. caroliniana* sens. Mett., Linnaea 20: 278. 1847. *A. mexicana* S. & C. 1830. nom. nud.**

This species possibly may be expected in Guatemala, as it occurs in Mexico, in South America from the Guianas to Bolivia, and in western and midwestern United States. One sterile collection has been tentatively determined by Svenson (1944) on the basis of general appearance, as well as one each fertile specimens from Honduras and Costa Rica. Diagnostic features of fertile material are the many-septate glochidia and the pitted surfaces of megaspores. Thus, it should not be confused with *A. filiculoides*, which has nonseptate glochidia and raised, rather than pitted, sculpturing of megaspores. Although glochidia of *A. mexicana* match those of *A. microphylla*, megaspores are pitted, not smooth.

SALVINIA Adanson

REFERENCES: Robert Herzog, Ein Beitrag zur Systematik der Gattung *Salvinia*, Hedwigia 74: 257–284. 1935. C. A. Weatherby, A further note on *Salvinia*, Amer. Fern J. 27: 98–102. 1937. E. R. de la Sota, Sinopsis de las especies Argentinas del genero *Salvinia*, Bol. Soc. Argent. Bot. 17: 47–50. 1976.

Plants with true roots lacking; rhizome horizontal, bearing alternate whorls of 3 leaves, 2 of them floating, 1 submerged; floating leaves green, entire, plane (or at first folded or, in an Asian species, cucullate), oblong-elliptic to nearly circular, the apex obtuse to retuse or emarginate, the base cordate or subcordate, the undersurface nearly naked to densely covered with septate trichomes, the upper surface covered with minute to conspicuous papillae, venation essentially pinnate, with primary veins spreading from the midrib and secondary veins copiously anastomosing to form numerous, minute areoles between the primary ones; submerged leaves highly divided into numerous rootlike filaments which trail through and draw nourishment from the water and bear, at their bases or along their margins, several to many sporocarps; sporocarps subglobose, containing either megasporangia or microsporangia enclosed within a thin-walled indusium; megasporangia short-stalked, each maturing only 1 megaspore; microsporangia longer-stalked, containing 64 trilete microspores.

Salvinia contains about a dozen species, mostly occurring in tropical or subtropical regions in both hemispheres. Two species are recognized in Guatemala:

- a. Papillae on floating leaves each bearing (usually) 4 septate trichomes which are joined at their tips; largest floating leaves 1.5–2.5 cm long, the apices obtuse or retuse; stele of the rhizome U-shaped in cross section. *S. auriculata*.
- a. Papillae with free trichomes, (i.e., not joined at their tips); largest floating leaves 0.6–1.2 (–1.3) cm long, the apices rarely (if ever) retuse; stele of the rhizome circular in cross section. *S. minima*.

Salvinia auriculata Aubl., Histoire des plantes Guiane Francoise 2: 969. 1775. *S. rotundifolia* Willd., in L., Species Plantarum, ed. 4, 5: 537. 1810.

Floating in lakes, or in river pools, sea level to 50 m; Izabal; Petén. Cuba; Jamaica; Mexico; Honduras south to Paraguay and northeastern Argentina.

Rhizome with stele U-shaped in cross section; floating leaves drying green to brown, oblong-elliptic to nearly circular, apex obtuse or retuse, base cordate or subcordate, larger ones 1.5–2.5 cm long, undersurface sparsely to moderately provided with minute, castaneous, septate trichomes, upper surface densely provided with short to greatly elongated papillae, these arranged in rows paralleling the main lateral veins and each of them developing at the apex a group of 4 trichomes which are all joined at their ends; submerged leaves (2–) 3–10 cm long; (none of the 20 specimens seen from Central America were fertile, but in collections examined from South America sporocarps were 1.5–2.5 mm in diameter).

In the past, some confusion existed as to application of the name *S. rotundifolia*. One such author was Weatherby (1937), who attempted to separate *S. rotundifolia*

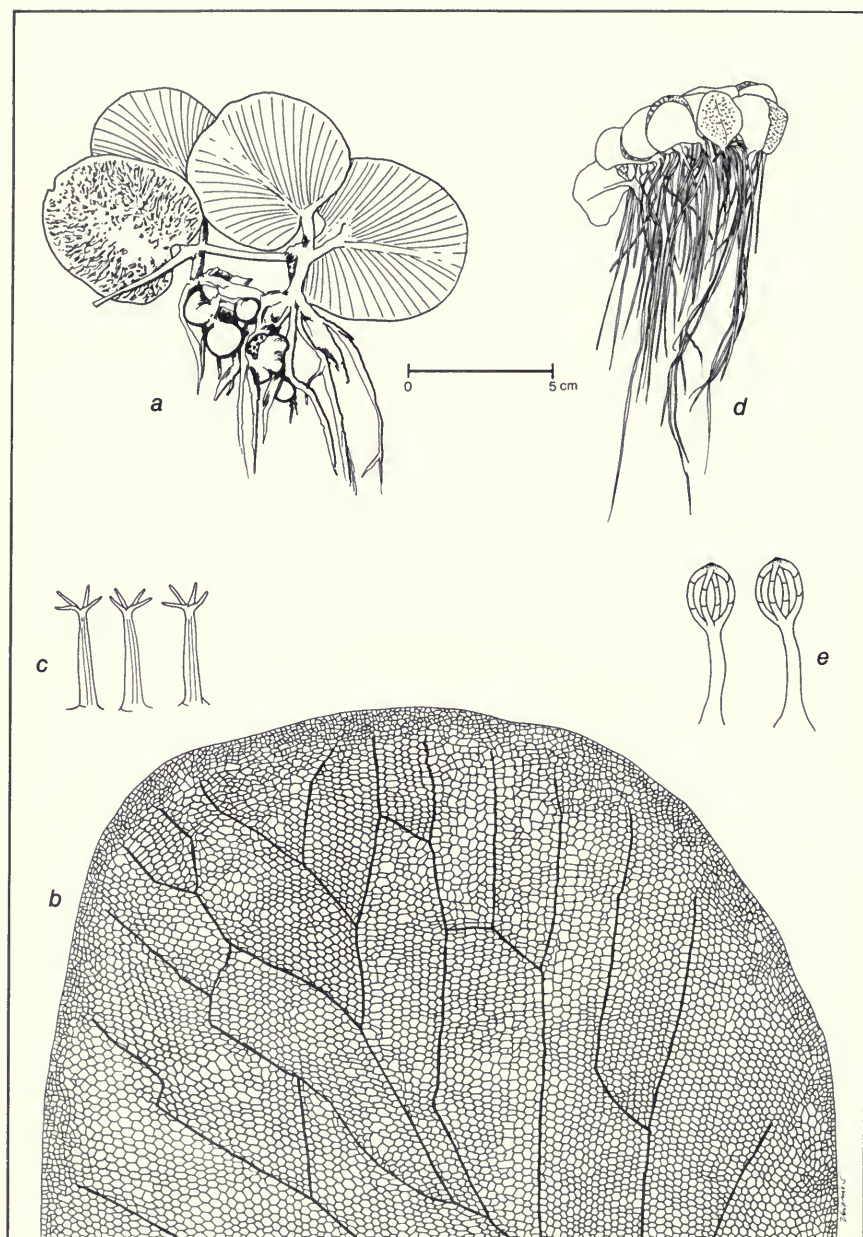


FIG. 3. *Salvinia*. a–c, *S. minima*: a, habit, $\times 3$; b, portion of leaf showing venation, $\times 25$; c, papillae with free, spreading trichomes, $\times 25$. d–e, *S. auriculata*: d, habit, $\times \frac{1}{2}$; e, papillae with joined trichomes, $\times 25$.

from *S. auriculata*, principally on the basis of free vs. joined trichomes on the leaf papillae. However, true *S. rotundifolia* Willd. was found by Morton (Contr. U.S. Natl. Herb. 38: 75. 1967) to be synonymous with *S. auriculata*, and those plants earlier mistaken as *S. rotundifolia* are now recognized as *S. minima*.

Some workers have also included *S. radula* under *S. auriculata*, either as a synonym or as a variety of it. For further discussion, see treatment of the former under "Dubious or Excluded Species."

***Salvinia minima* Bak., J. Bot. 24: 98. 1886.**

Floating in lakes, ponds, swamps, and quiet backwaters of streams and rivers, sea level to 1,200 m; Alta Verapaz; Escuintla; Guatemala; Izabal; Jutiapa; Petén; Sacatepéquez; Santa Rosa. Southeastern United States; Minnesota (perhaps introduced); Mexico; British Honduras; Honduras south to Argentina and Uruguay.

Rhizome with stele circular in cross section; floating leaves, mostly drying green or olive-green to brownish, oblong-elliptic, apex obtuse (not or rarely retuse), base cordate, larger ones 0.6–1.2 (–1.3) cm long, undersurface moderately to (commonly) densely provided with castaneous, septate trichomes, upper surface densely provided with elongated papillae, these arranged in rows paralleling the main lateral veins and each of them developing at the apex a group of 4 trichomes which are all free at their tips; submerged leaves 0.5–4.5 (–5.5) cm long; sporocarps 0.8–1.5 mm in diameter, scattered along the branches of fertile leaves. (Only 2 of 30 specimens examined from Guatemala were fertile!)

A majority of the Central American collections of *S. minima* seen in various herbaria were determined as *S. rotundifolia*. The latter name has proven to be synonymous with *S. auriculata*. See discussion of the latter for further details.

DUBIOUS OR EXCLUDED SPECIES

***Salvinia radula* Bak., J. Bot. 24: 98. 1886.**

Disagreement has arisen as to the position of this species. Herzog (1935) placed it with *S. auriculata*, but Weatherby (1937) insisted that *S. radula* differed in the generally smaller size of its floating leaves, in the papillae being reduced or obsolete, and in the presence of single trichomes scattered between the papillae. According to Weatherby, *S. radula* was found in Panama, Cuba, the Guianas, and Ecuador. He also annotated two Guatemalan specimens at U.S. National Herbarium: *Harry Johnson* 315, from Lago Izabal, as *S. auriculata* "approaching *S. radula*"; and *S. F. Blake* 7849, from Rio Izabal as *S. radula*. However, although both specimens have rather small floating leaves, both have conspicuous papillae, and neither show indications of single trichomes between papillae. Whether this entity merits specific distinction is still problematical. If so, it might be expected to turn up in Guatemala. Further collections are needed, especially of fertile plants. Type material, according to Weatherby, is as yet undesignated.

PSILOTACEAE

REFERENCES: Clyde F. Reed, Index Psilotales, Bol. Soc. Brot. 40: 71–96. 1966. D. W. Bierhorst, Psilotaceae and Noeggerathiaceae (pp. 153–192), in *Morphology of Vascular Plants*, Macmillan Company, New York, 1971. G. Brownlie, Psilotaceae (pp. 11–15), in *The pteridophyte flora of Fiji*, Cramer, Federal Republic of Germany, 1977. W. H. Wagner, Systematic implications of the Psilotaceae, Brittonia 29: 54–63. 1977.

Plants terrestrial or epiphytic, lacking roots; rhizome creeping, branched, mycorrhizal; aerial shoots erect or pendent, simple or (in ours) repeatedly dichotomous; leaves small, in ours reduced to minute appendages, not circinate in vernation, the barren ones simple, the fertile ones forked or bifid; spores borne in a bi- or trilocular synangium which is attached to the short stalk of the fertile appendage (sporangiophore); spores monolete, reniform or fabiform, without perine.

One of the most primitive of all plant families, the Psilotaceae consists of two genera: *Psilotum*, with two pantropical species, and *Tmesipteris*, with about 10 species occurring chiefly in Australia, New Zealand, and some South Pacific islands.

PSILOTUM Swartz

Plants epiphytic, epipetric, or sometimes terrestrial; aerial shoots erect to pendent, repeatedly dichotomous, especially in the distal half, the primary axis and branches flattened or triquetrous, dark or yellowish green; leaves reduced to minute appendages (sporangiophores), ca. 1 mm long, barren ones simple, sessile, triangular, fertile ones forked; synangia trilocular, subsessile or on very short, thick stalks.

The genus, represented by two closely related species, occurs in tropical or subtropical regions around the world. Intermediates (probably with abnormal spores) are to be expected where the two species grow together, e.g., in Oahu, Hawaii (*vide* Wagner: Interspecific crosses and spore characteristics in the genus *Psilotum*, Amer. J. Bot. 49: 680. 1962).

- a. Branches triquetrous; sporangiophores (especially distal ones) borne spirally, triseriate.
P. nudum.
- a. Branches flattened; sporangiophores borne in subopposite or alternate pairs.
P. complanatum.

***Psilotum complanatum* Sw.**, Syn. Fil. 188, t. 4, f. 5. 1806. *P. flaccidum* Wall. Cat. 45. 1828.

Apparently known in Guatemala from a single collection, *Steyermark* 31230, "dry crevices of boulders. . . and on vertical cliffs," Montaña Castilla, 3 mi southeast of Quezaltepeque, altitude 1,200–1,500 m; elsewhere, on trees or rocky cliffs or ravine banks; Mexico; Honduras; El Salvador; Greater Antilles; Colombia; Venezuela; Peru; Old World Tropics.

Plants (at least in Central America) epipetric; aerial shoots erect to (mostly) pendent, 15–50 cm long, or to 100 cm long in the Old World; branches commonly 1–2 mm broad, flattened, yellowish green; sporangiophores borne in alternate or subopposite pairs on the margins of branches.

Besides the characters used in the key, *P. complanatum* often can be distinguished from *P. nudum* on the consistently pale, yellow-green color of the branches. Branches of the latter are occasionally pale in hue, but are typically dark or grayish green.

***Psilotum nudum* (L.) Pal.-Beauv.**, Prodrôme Aethéogamie 106, 112. 1805. *Lycopodium nudum* L., Species Plantarum 1100. 1753. *P. triquetrum* Sw., in J. Bot. (Schrader) 1800(2): 109. 1802. *P. floridanum* Michx., Fl. Bor. Amer. 2: 281. 1803.

In thickets, open forests and clearings, on trunks of trees or in rocky crevices of cliffs, sea level to 1,300 m; Alta Verapaz; Chiquimula; Izabal. Southeastern United States (South Carolina and Florida); West Indies; Mexico; British Honduras; Hon-

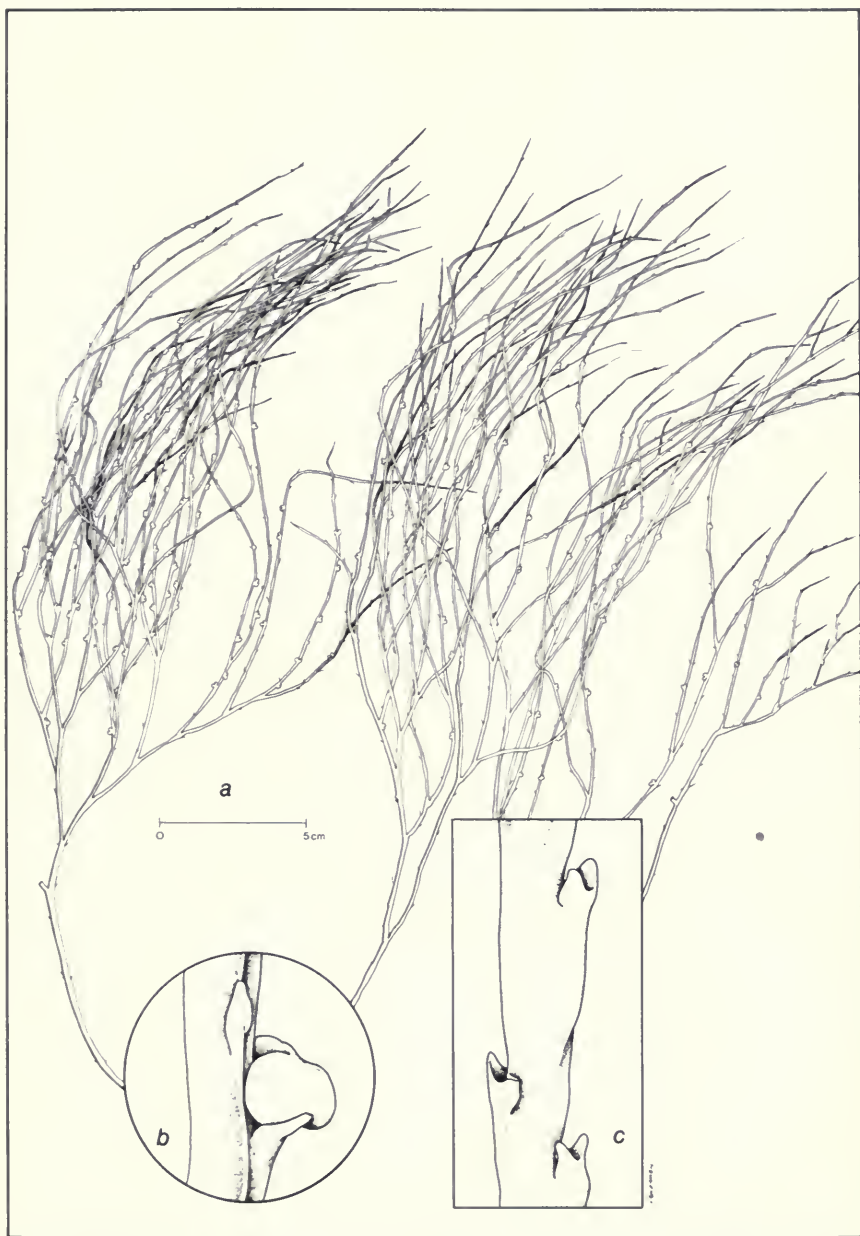


FIG. 4. *Psilotum*. a–b, *P. nudum*: a, habit, $\times \frac{1}{2}$; b, portion of fertile branch with sporangium, $\times 9$. c, *P. complanatum*, portion of sterile branch, $\times 9$.

duras; Costa Rica (Cocos Island); Panama; Colombia; Venezuela; Ecuador; Peru; Brazil; Paraguay; Argentina; Old World Tropics.

Plants epiphytic or epipetric; aerial shoots arching or pendent, 15–60 cm long; branches 0.7–1.7 mm broad, triquetrous (at least distally), yellowish or (typically) grayish green; sporangiophores (especially distal ones) borne spirally along the ridges of branches, mostly triseriate.

EQUISETACEAE

Plants terrestrial, rushlike, small and inconspicuous to 8 m tall; rhizomes perennial, extensively branched and creeping, with villous roots; aerial stems perennial or annual, erect, cylindrical, conspicuously jointed, irregularly branched, or (in ours) simple or with whorled branches springing from the nodes, hollow between the nodes, with a large central cavity surrounded by a number of smaller ones, the surface shallowly to conspicuously ridged, the ridges and grooves variously coated with silica arranged in patterns or forming tubercles, stomata forming lines or broader bands in the grooves; leaves minute, reduced to toothed scales which form sheaths surrounding the stem nodes, the teeth persistent to early-deciduous; sporophylls forming a strobilus at the apex of stem or branch, each sporophyll stalked and terminated by a protective hexagonal shield, from which are suspended 5–6 elongated sporangia; normal spores chlorophyllous, spherical, lacking surface ornamentation, but bearing 4 hygroscopic, armlike elaters which coil and uncoil in the presence or absence of moisture and which evidently aid in spore dispersal.

EQUISETUM Linnaeus

REFERENCES: J. Milde, *Monographia Equisetorum*, Nov. Actorum Acad. Caes. Leop.-Carol. German. Nat. Cur. 32(2). 1867. J. H. Schaffner, North American species of *Equisetum* north of Mexico, Amer. Fern J. 11: 65–75. 1921; and Diagnostic key to the species of *Equisetum*, *op. cit.* 22: 69–75, 122–128. 1932. R. Hauke, A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*, Beih. Nova Hedwigia 8: 1–123. 1963.

Characters are those of the family.

Although the “horsetail” can easily be distinguished from all other plants, problems of species delimitation within the genus are severe. Among the few diagnostic characters available, most are microscopic or are obfuscated by extensive hybridization. Moreover, a certain degree of familiarization with the genus is necessary before one can begin to appreciate the nature of the characters. So when attempting to determine a new collection, one must understand that a cursory glance can often result in an incorrect identification; also, the odds of having in hand a hybrid plant are quite high. For example, among all the specimens examined from Guatemala for this study, the number of collections of the two hybrids far exceeded those of two of the putative parents, *E. giganteum* and *E. hyemale*. Hybrid plants often bear strobili, especially on the branch tips, but the spores are presumed nonviable. Such spores either lack elaters, or these are only partly developed and are appressed to the spore body. Furthermore, normal spores are colored a beautiful, clear green, whereas abortive spores lack chlorophyll.

The following key treats only the three true species of *Equisetum* which occur in Guatemala. However, immediately following the descriptions of these are discussions of the two hybrids that may be expected here. The reader is urged to use both key and discussions in attempting to identify collections.

- a. Stems normally unbranched; sheaths girdled with dark brown or black (at least when mature). *E. hyemale* var. *affine*.

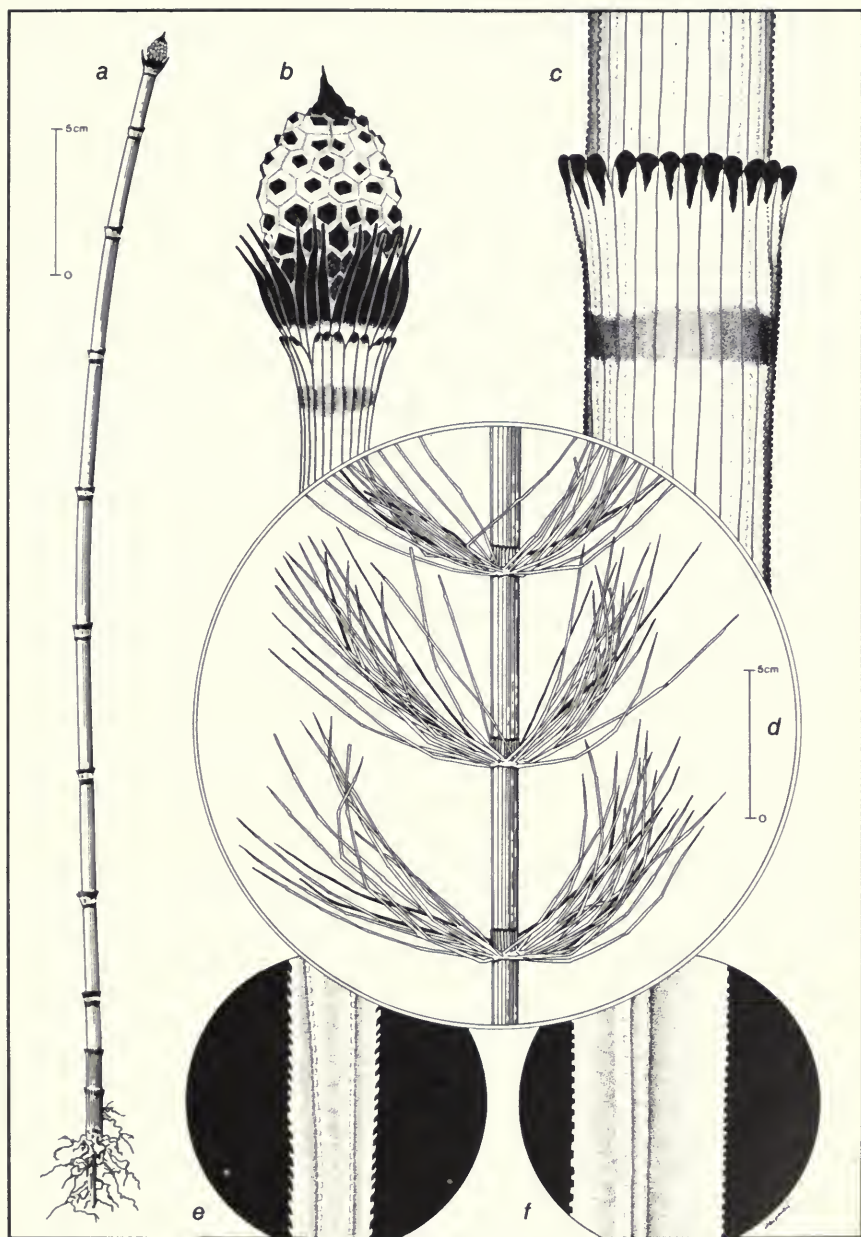


FIG. 5. *Equisetum*. a–c, *E. hyemale* var. *affine*: a, habit, $\times \frac{1}{2}$; b, strobilus, $\times 4 \frac{1}{2}$; c, stem sheath, $\times 18$. d–e, *E. myriochaetum*: d, portion of main stem with whorled branches, $\times \frac{1}{2}$; e, portion of branch with ridge teeth in profile, $\times 19$. f, *E. giganteum*, portion of branch with ridge teeth in profile, $\times 19$.

- a. Stems producing regular whorls of branches at the nodes; sheaths the same color as the stem, or proximal ones wholly light brown (but not dark-girdled).
- b. Tubercles along the ridges of branches appearing (in profile) like sawteeth, the teeth pointed toward branch apex; stomata in a single line on each side of the groove; stem sheaths all colored the same as the stem. *E. myriochaetum*.
- b. Tubercles of branch ridges appearing square or flattened, in profile; stomata in (2-) 3-4 lines along the flanks of grooves; stem sheaths (proximal ones) often light brown. *E. giganteum*.

***Equisetum giganteum* L.**, Species Plantarum 1517. 1763. *E. ramosissimum* H.B.K., in Willd., Species Plantarum, ed. 4, 5: 9. 1810 (not Desf. 1800). *E. xylochaetum* Mett., Filices Lechlerianae 2: 34. 1859.

In moist places, in forests, thickets or in open fields, 500-900 m; Escuintla; Sacatepéquez; San Marcos; Santa Rosa. Honduras to Chile; Cuba; Jamaica; Hispaniola.

Stems stout, to 3 m tall (in Guatemala; elsewhere to 5 m) and 20 mm in diameter, with regular whorls of branches at the nodes, stomata in (2-) 3-4 lines along the flanks of the stem grooves; sheaths green, or proximal ones light brown, commonly cylindrical and about as broad as long, regularly appressed to the stem, the teeth white, or brown with white margins, persistent to early-deciduous; branches numerous, 8-10-ridged, the tubercles on the ridges appearing square or flattened, in profile; strobili shortly but distinctly apiculate, borne at the apices of branches, and occasionally at the apex of the young stem; spores green.

Often, in various herbaria, specimens of *Equisetum* with regularly whorled branches can be found incorrectly identified as *E. giganteum* when, in truth, they are either *E. myriochaetum* or the hybrid *E. × schaffneri*. Actually, *E. giganteum* is rather infrequent in Guatemala. It is *E. myriochaetum* which is the most common species here as well as throughout Central America. See treatment of *E. myriochaetum* for further discussion.

***Equisetum hyemale* L. var. *affine* (Engelm.) A. A. Eaton**, Fern Bull. 11: 111. 1903 ("*E. hiemale*"). *E. prealtum* Raf., Flora Ludoviciana 13. 1817 ("*E. praealtum*"). *E. prealtum* var. *affine* (Engelm.) Broun, Index to North American Ferns 89. 1938. *Rismachq'ij; kolo macho ujekiej; cola de caballo*.

In shallow waters of streams, on moist slopes, or in wet meadows, thickets or ravines, 1,600-2,700 m; Chimaltenango; Huehuetenango; Sacatepéquez; Sololá. Southern Mexico; United States and Canada; pacific coast of Asia.

Stems normally unbranched (occasionally branching at injured areas), 0.2-2 m tall, in ours 2-8 mm in diameter, stomata in a single line along the side of each groove; sheaths (at least mature ones) with a dark brown to blackish girdle around the middle, constricted near base, appressed to flaring at apex, the teeth castaneous to white, or castaneous with white margins, somewhat persistent to early deciduous; strobili prominently apiculate; spores green.

With its unbranched stems and dark-girdled sheaths, this cannot be confused with other species in Guatemala. Our variety can scarcely be distinguished from the typical, which supposedly differs in smaller stem size and yet in slightly longer sheaths, in its always early deciduous sheath teeth (vs. sometimes persistent in var. *affine*), and its always bituberculate ridges (vs. sometimes bituberculate ridges in var. *affine*). The typical variety is apparently confined to Eurasia.

Frequent hybridization occurs between *E. hyemale* var. *affine* and *E. myriochaetum* throughout the range of distribution. See discussion of hybrids which follows below.

Equisetum hyemale has sometimes been used in Guatemala as a native remedy for inflammation, diarrhea, and kidney pain.

Equisetum myriochaetum Schlecht. & Cham., Linnaea 5: 623. 1830. *E. mexicanum* Milde, Verh. K.K. Zool.-Bot. Ges. Wien 11: 355. 1861. *S-solol amoc* (frog's throat); *cola de caballo*; *barba viejo* (*vide* Steyermark, Huehuetenango).

In forests, thickets, shaded ravines, open banks and meadows, in and along banks of streams and rivers, in swamps and marshes, 250–2,100 m; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Huehuetenango; Quezaltenango; El Quiché; Sololá; Zacapa. Mexico to Panama; Colombia; Ecuador; Peru.

Stems stout, to 4 m tall (in Guatemala; elsewhere to 8 m) and 15 mm in diameter, with regular whorls of branches at the nodes, stomata in a single line on each side of the stem grooves; sheaths all green, commonly cylindrical and about as broad as long, regularly appressed to the stem, the teeth brown to white, persistent to early-deciduous; branches numerous, 6–8-ridged, the tubercles on the ridges appearing (in profile) like sawteeth, the teeth pointed toward branch apex; strobili borne at the apices of stems and branches, blunt, or those of the branches with a slight apiculum; spores green.

In Huehuetenango, this species is reported to be boiled and the infusion drunk in the treatment of kidney disorders (*vide* Steyermark).

This is the most common species of *Equisetum* throughout Central America. Before Hauke's (1963) revision of subgenus *Hippochaete*, specimens were frequently misidentified as *E. giganteum* or one of the several hybrids. The simplest and quickest means of separating the two species is by the character of the profile of branch ridges, as noted in the key. In fertile specimens, the strobili are of further help, those of *E. giganteum* being minutely but distinctly apiculate, whereas in *E. myriochaetum* (at least in Guatemala), they are blunt, or those of the branches occasionally with an inconspicuous apiculum.

Equisetum myriochaetum hybridizes readily with both *E. giganteum* and *E. hyemale*, which adds to the difficulties of identification in the genus. See discussion of the various hybrids which follows below.

EQUISETUM HYBRIDS

To add to the confusion which already exists in the identification of species of *Equisetum*, there is the problem of frequent hybridization. Hauke (1963) lists six hybrids in his revision of subgenus *Hippochaete*, two of which are known to occur in Guatemala.

Equisetum hyemale var. *affine* × *myriochaetum*.

Stems are usually stout and most often resemble *E. myriochaetum* in their abundant branches; but often the branches are scattered and irregular, or occasionally they may be essentially lacking, as in *E. hyemale*. The stem sheath is usually the best diagnostic character in this hybrid, a perfectly intermediate condition between that of the putative parents: commonly the sheaths in the distal half are the same color as the stem (as in *E. myriochaetum*), but girdled with dark brown or black proximally (as in *E. hyemale*). If branches are present, the ridges bear tubercles which are irregularly shaped or slightly to conspicuously sawtoothed. Strobili also may be present, these distinctly apiculate (as in *E. hyemale*), but the spores are malformed and lack chlorophyll.

Numerous collections have been made and documented in Guatemala, occurring between 200 and 1,800 m, in Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez; Sololá; Zacapa. The hybrid also occurs in Mexico.

Equisetum × *schaffneri* Milde, Verh. K.K. Zool.-Bot. Ges. Wien 11: 345. 1861 (to species).

Putative parents are *E. giganteum* and *E. myriochaetum* and, curiously, collections of the hybrid thus far greatly outnumber those of *E. giganteum* in Guatemala. It may be distinguished from both species only with difficulty, as it closely resembles both in many ways: the large stems, the abundance of whorled branches, and the tightly appressed, cylindrical sheaths nearly as broad as long, with their brown to white, persistent to deciduous teeth. It is perfectly intermediate between the two in the apex of strobili and pattern of stomata. In *E. giganteum*, strobili are minutely but distinctly apiculate, and stomata are arranged regularly in three to four lines on the flanks of the grooves. In *E. myriochaetum*, strobili are blunt and stomata are in single lines on each side of the groove. However, in *E. × schaffneri*, strobili are acute to slightly apiculate, and stomata are irregularly patterned, in one to two or three lines. The hybrid more closely resembles *E. myriochaetum* in the profile of ridge tubercles of the branches (sawtoothed to somewhat irregular, *never* squared or flattened) and in the sheaths having the same color as the stem (not light brown toward the base as frequently occurs in *E. giganteum*). *Equisetum* × *schaffneri* often bears strobili on the branch tips, but spores are malformed and lack chlorophyll.

LYCOPODIACEAE

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Perennial, terrestrial or epiphytic herbs, mostly of moderate size, with erect, ascending, creeping, scandent, or pendent, dichotomously branched shoots; dichotomies equal throughout and the branches usually similar or unequal, and the branches differentiated into indeterminate, long-creeping main stems and shorter, usually determinate, branchlet systems; roots appearing as a basal tuft or along the underside of main stems; leaves microphyllous, small, simple, with a single vein, in spiral, decussate, or whorled arrangement, all similar, or anisophyllous or heterophyllous; sporophylls like other leaves, or modified, sometimes aggregated into distinct strobili; sporangia solitary in leaf axils or on the upper side of the sporophyll base, unilocular, reniform or subglobular, sessile, or short-stalked, opening by a transverse slit into 2 equal or strongly unequal valves; spores

all of one kind, subglobose to tetrahedral, with a trilete scar; gametophytes tuberous, subterranean and saprophytic, or epigenous and green, monoecious.

As treated here, Lycopodiaceae is a family of two genera, *Lycopodium* and *Phylloglossum*. Authors have had different opinions of the rank of the segregates in the family, accepting from two to 12 genera. The genus *Lycopodium* is here maintained in the broadest sense, and its segregates are given as subgenera, some of which may be further subdivided into sections. However, it should be noted that the differences separating these are probably equally or even more profound than the characteristics separating many well-established genera of the Lycopodiaceae, for instance. On the other hand, the most distinct diagnostic characters which separate the segregates in *Lycopodium* are either microscopic (spores, sporangium wall cells, chromosome numbers, mucilage canals) or very rarely seen (gametophytes) and therefore not so useful for identification purposes.

Only *Lycopodium* is represented in Guatemala. The other genus, *Phylloglossum*, is in Australia and New Zealand.

LYCOPODIUM Linnaeus

Characters are those given for the family above.

As circumscribed here, *Lycopodium* is a cosmopolitan genus containing perhaps 400 species, the majority of which occur in moist or wet tropical or subtropical regions. About half of the species are found in the American Tropics, and 24 species are recognized for Guatemala.

The following key separates the Guatemalan species into their subgenera. Treatments of the subgenera then follow in alphabetical order.

- a. Dichotomies equal throughout, the branches similar, without elongate main stems; roots forming a basal tuft; sporophylls and ordinary leaves alike, or sporophylls, if smaller, not subpeltate. subg. SELAGO, p. 28.
- a. Dichotomies unequal, the branches differentiated into elongate, horizontal main stems and ascending or upright lateral branchlet systems, or simple peduncles; roots emerging with intervals along the underside of horizontal stems; sporophylls strongly modified, subpeltate, aggregated in terminal, compact strobili.
 - b. Strobili nodding or pendent, terminating the branchlets of upright treelike branch systems. subg. CERNUISTACHYS, p. 21.
 - b. Strobili erect.
 - c. Strobilus-bearing branch arising from a branchlet system which is laterally situated on the horizontal main stem; strobili on branched, or rarely simple, peduncles. subg. LYCOPodium, p. 25.
 - c. Strobilus-bearing branch arising directly from the upper side of the creeping stem, unbranched. subg. CERNUISTACHYS, p. 21.

LYCOPodium subg. **CERNUISTACHYS** Herter, Bot. Jahrb. Syst. 43, Beibl. 98: 29. 1909 (as *Cernuostachys*). *Lycopodiella* Holub, Preslia 36: 20, 22. 1964; emend. Pichi-Sermolli, Webbia 23: 164. 1968. *Lycopodium* subg. *Lycopodiella* (Holub) B. Øllgaard, Amer. Fern J. 69: 49. 1979.

Plants terrestrial, unequally dichotomous, with horizontal, indeterminate main stems, rooting along the underside, sometimes with long intervals, bearing erect branches arising on the upper side, and laterally arising horizontal branchlet systems; erect branches either simple and terminating in a single erect strobilus, or profusely branched, forming a treelike branch system with nodding or pendent strobili terminating the branchlets of the horizontally spreading branchlet systems of the erect main branch; sporophylls subpeltate, with a thin decurrent-adnate median wing; sporangia reniform or subglobose, sessile on the

sporophyll base, opening into 2 equal or strongly unequal valves, the wall cells nonsinuate, unligified except for the nodular or semiannular thickenings; spores rugate, with anastomosing rounded ridges and undulations; gametophytes epigenous, green.

A subgenus of perhaps 40 species in almost all moist temperate and tropical regions. About two-thirds of the species occur in the Americas, and South America especially has a high diversity. Only three species are found in Guatemala, representing three of the four sections. Section *Lateralia* Baker (New Zealand to the Philippines) has a deviating branching pattern which was excluded from the description above.

Subgenus *Cernuistachys* has frequently been treated as the genus *Lepidotis* Pal.-Beauv., emend. Rothmaler (1944), or as subgenus *Lepidotis* (Pal.-Beauv.) Baker. Unfortunately, this name cannot be used because it is lectotypified by *Lycopodium clavatum* L., which is the type species of *Lycopodium* L. At the genus level, the correct name is *Lycopodiella*.

The species with scandent growth and treelike branching (sect. *Cernua* [Baker] Pritzel) have a striking and unique appearance in the subgenus, and a separate genus *Palhinhaea* Franco & Vasconcellos, in Vasconcellos & Franco, has been erected for them. However, the whole subgenus is strikingly similar in several distinct microscopic characters and in gametophyte morphology.

- a. Plants much-branched, with upright treelike branch systems, bearing numerous small pendent or nodding strobili, and arching-scandent, trailing shoots. *L. cernuum*.
- a. Plants sparsely branched, with simple upright peduncles, bearing a single large, erect strobilus each, and short creeping to arching horizontal shoots.
 - b. Leaves of horizontal shoots uniform; leaves of the erect branch in numerous ranks, densely covering the stem; sporophylls slightly broader than lower leaves.
 - L. alopecuroides*.
 - b. Leaves of horizontal shoots dimorphic, the lateral ones broad and long, the upper ones shorter and narrow; leaves of the erect branch (peduncle) small, acicular, in remote, alternating whorls of 4, not covering the stem; sporophylls broad, subpeltate. *L. carolinianum* var. *meridionale*.

***Lycopodium alopecuroides* L., Species Plantarum 1102. 1753. *Plananthus alopecuroides* (L.) Pal.-Beauv., Prodrôme Aethéogamie 111. 1805. *Lepidotis alopecuroides* (L.) Rothmaler, Feddes Repert. Spec. Nov. Regni Veg. 54: 66. 1944. *Lycopodiella alopecuroides* (L.) Cranfill, Amer. Fern J. 71: 97. 1981.**

Wet, springy meadows and moist banks, altitude ca. 1,800 m; El Quiché. South-eastern United States; Cuba; Hispaniola; Central America; tropical South America.

Plants with the horizontal stem arching or appressed to the ground, firmly rooted with short intervals, bearing stiffly erect, simple, strobiliferous branches directly on the upper side; horizontal stems 10–25 cm long, sparsely and unequally branched, densely covered on all sides by uniform, somewhat upwardly second or spreading to perpendicular leaves, 7–12 mm broad including the leaves; leaves narrowly lanceolate to subulate, flat, with smooth or denticulate-ciliate margins, soft, light green, 5–8 mm long, 0.5–1 mm broad at the base; erect branch ca. 5–8 mm in diameter including leaves, 10–15 (–30) cm high with the strobilus, its leaves radially arranged, in alternating whorls of 6 or more, ca. 1 mm apart, forming 12 or more indistinct longitudinal ranks, like the leaves of horizontal shoots, or slightly narrower, usually more ascending; strobilus 2.5–4 (–10) cm long, 10–12 (–18) mm in diameter including sporophylls, only slightly thicker than its peduncle; sporophylls arranged as leaves of the peduncle, narrowly lanceolate from a narrow, subpeltate base, with many spreading-hooked teeth on the margins, 5–8 mm long, ca. 1 mm broad at the base; sporangia subglobose, ca. 1 mm in diameter, very soft, almost completely enclosed by sporophyll bases, opening by strongly unequal valves.

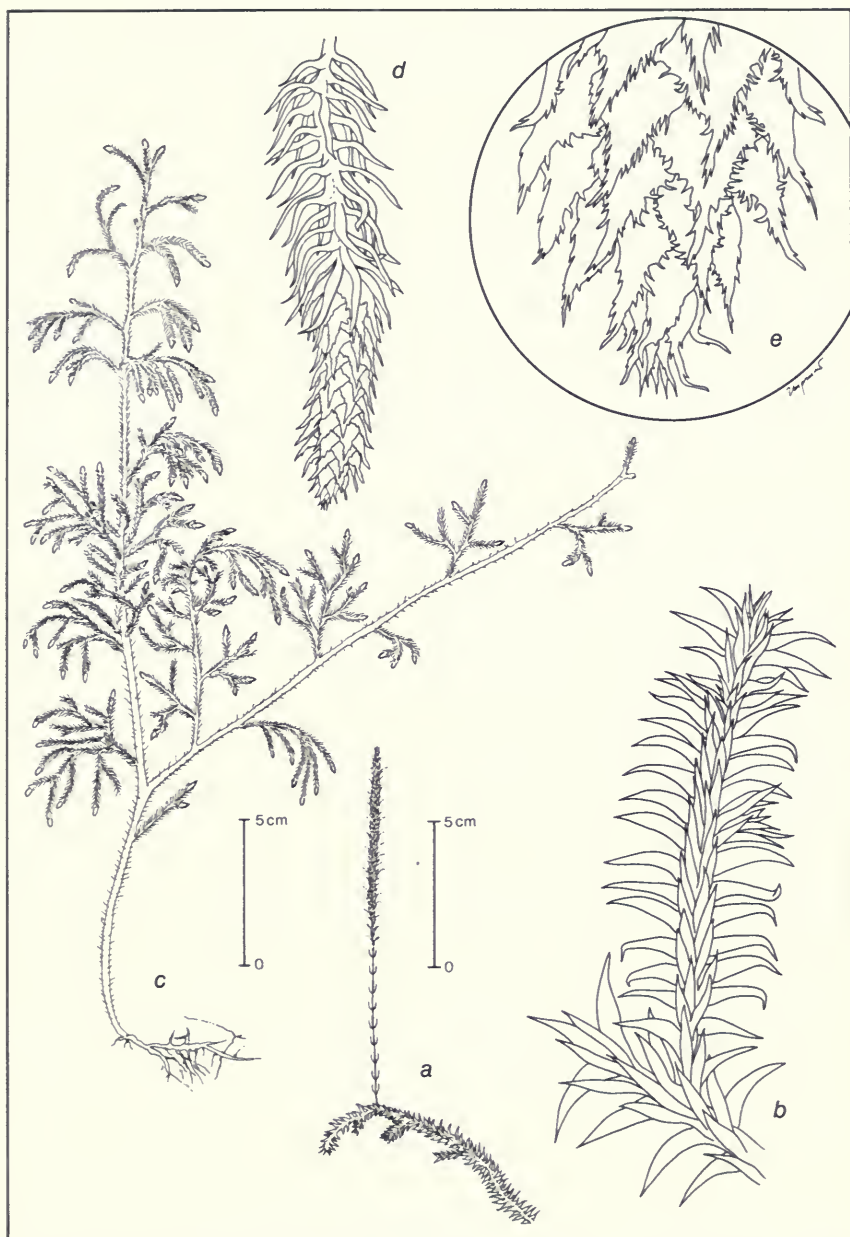


FIG. 6. *Lycopodium* subgenus *Cernuistachys*. a–b, *L. carolinianum* var. *meridionale*: a, habit, $\times \frac{1}{2}$; b, portion of stem and branch, $\times 3$. c–e, *L. cernuum*: c, habit, $\times \frac{1}{2}$; d, ultimate branchlet, showing sterile leaves and strobilus, $\times 6$; e, apex of strobilus, $\times 25$.

Lycopodium alopecuroides is known only from two collections in Guatemala. The description above is based on these, but supplemented by some measurements (in parentheses) from other parts of its tropical range. The name is here used in a broad sense, because the relation of the Guatemalan specimens to members of the whole species complex in both temperate North America and tropical America is unresolved. The taxonomy of the group is very poorly understood in tropical America. The type of *L. alopecuroides* is from eastern temperate North America.

Lycopodium carolinianum* L., Species Plantarum 1104. 1753, var. *meridionale (Underw. & Lloyd) Nessel & Hoehne, Arch. Bot. São Paulo 1: 431. 1927. *L. meridionale* Underw. & Lloyd, Bull. Torrey Bot. Club 33: 121. 1906.

In savanna, open swampy ground, swampy pine forest, from sea level to ca. 900 m. Escuintla, one collection. Antilles; Mexico (Tabasco); British Honduras to Nicaragua; tropical South America, but rare in the Andes.

Plants terrestrial, with horizontal stems creeping and firmly rooted, bearing usually 1 stiffly erect, simple, strobilus-bearing branch (peduncle) directly on the upper side; creeping stems 10–15 cm long, sparsely and unequally branched, covered by leaves, 10–15 mm broad including leaves, 1–2 mm thick excluding leaves; leaves of creeping stems dimorphic, in 2 lateral and 3–4 indistinct dorsal ranks; lateral leaves oblique-spreading, decurved-falcate, 6–8 mm long, 1–2.5 mm broad at the base, tapering into a long, pointed apex, flat, with smooth margins; dorsal leaves lanceolate-subulate, almost straight, or curved upward and appressed, 2.5–5 mm long, 0.8–1 mm broad at the base; peduncle up to 35 cm high including the strobilus, 1–1.5 mm thick, terete, bearing small (ca. 3 mm long) acicular leaves in remote, alternating, irregular whorls of 4, the distance between whorls 4–8 mm; strobili 2.5–10 cm long, ca. 3 mm in diameter excluding spreading sporophyll tips, or 7–8 mm including these; sporophylls borne in alternating whorls of 4, forming 8 longitudinal ranks, subpeltate, with a narrowly rhombic-acuminate, flattened exterior face, 3–4 mm long, ca. 2 mm broad, with the base adnate to the strobilus axis with a thin, median, decurrent wing, the tips spreading at maturity, with subscarios, erose-denticulate margins; sporangia reniform, almost fully exposed at maturity, ca. 1.5 mm broad, opening by almost equal valves.

This species is common in British Honduras and is expected to occur also in adjacent parts of Petén province.

Variety *meridionale* differs from the type variety mainly in its greater size. The number of leaves in the whorls of the peduncle and strobilus is generally larger, four vs. three in the type variety. As pointed out by Proctor (1977, p. 33), the characters originally used to separate this taxon are variable.

It is doubtful whether the African *L. affine* Bory and tropical Asian *L. carolinianum* can be maintained separate from *L. carolinianum* var. *meridionale*.

***Lycopodium cernuum* L., Species Plantarum 1103. 1753. *Lepidotis cernua* (L.) Pal.-Beauv., Prodrome Aethéogamie 101. 1805. *Lycopodium capillaceum* (Spring) Hieron., Bot. Jahrb. Syst. 34: 573. 1905. *Palhinhaea cernua* (L.) Franco & Vasc., in Vasc. & Franco, Bol. Soc. Brot. 41: 25. 1967. *Lycopodiella cernua* (L.) Pichi-Sermolli, Webbia 23: 165. 1968.**

Terrestrial, common as a pioneer plant on disturbed soil: sand, gravel or clay banks along roads and rivers, forest clearings, etc., from sea level to 2,600 m, also around fumaroles at 3,550 m; Alta Verapaz; Chiquimula; Esquintla; Huehuetenango; Izabal; El Progreso; Quezaltenango; San Marcos; Sololá; Suchitepéquez; Zacapa. Pantropic.

Plants with long, arching to scandent horizontal main shoots, rooting at long intervals, bearing strongly branched, treelike upright shoots 20–100 cm high which arise from the dorsal side of the arches; main axes of upright and arching shoots slender to robust, 2–6 mm thick excluding leaves; arching shoot with horizontal branchlet systems arising alternately to left and right; upright shoot bearing numerous subopposite, subdecussate, highly compound, spreading to horizontal, 5–15 (–20) cm long branchlet systems; ultimate branchlets nodding to drooping, 3–4 (–6) mm in diameter including leaves; leaves usually in alternating whorls of 3–5, forming 6–10 indistinct longitudinal ranks, or in low spirals, usually 3–4 mm long, thin, terete and acicular, or angular when dried, with conspicuous acroscopically adnate and decurrent leaf bases, changing gradually from patent-reflexed and rather distant on main stems, to patent, falcately ascending and densely crowded in ultimate branchlets, occasionally with sparse, lax hairs or minute spinules; the leaf bases often with longer, irregularly crisped or branched hairs, these rarely also on the surfaces of main stems; strobili usually numerous, terminating ultimate branchlets, sessile, narrower than the branchlet, cylindrical, 4–10 (–20) mm long, 2.5–3 mm in diameter, sporophylls usually in 10 ranks, ovate-peltate, short- to long-cuspidate, ca. 2 mm long, ca. 1 mm broad, partly scarious, yellowish or greenish, with coarsely erose-laciniate margins; sporangia almost completely enclosed by sporophyll bases, subglobose, 0.5–0.8 mm broad, soft, opening by strongly unequal valves.

Lycopodium cernuum is common and fairly uniform in Guatemala. Nessel (1939) recognized more than 40 varieties of this species. A few of these apply to Central American plants, but they seem indistinguishable from typical *L. cernuum*.

LYCOPODIUM subg. **LYCOPODIUM**. *Lycopodium* subg. *Rhopalostachya* Pritzel sect. *Clavata* Baker ex Pritzel, in Engler & Prantl, Die Natürlichen Pflanzenfamilien 1(4): 603. 1900. *Lycopodium* subg. *Acrostachys* Herter, Bot. Arch. 3: 19. 1923.

Plants terrestrial, unequally dichotomous, with indeterminate, elongate, trailing main stems (rhizomes), rooting at intervals along the underside, bearing usually determinate, ascending to upright, laterally arising branch systems from which strobili or peduncles arise; lateral branch systems repeatedly, unequally, bilaterally branched; strobili erect, either terminating the stronger branchlets or borne on simple or forked peduncles; sporophylls subpeltate with a thin basal, decurrent-adnate, median wing; sporangia reniform, sessile on the sporophyll base, opening by equal valves, the wall cells lignified, sinuate, without true partial thickenings, but the side walls of some species with pocket-like in- and exvaginations; spores reticulate, with thin sharp ridges; gametophytes subterranean, saprophytic.

A subgenus of perhaps 40 species, mainly in temperate regions of both the Northern and Southern Hemispheres, with less than 10 species in the American Tropics.

Of the seven sections belonging here, three Old World ones (southeast Asia to New Zealand) possess some deviating characters not included in the description above. These are, for instance: liana habit, nonpeltate sporophylls, unequal sporangium valves, and baculate or scabrate spores.

The two species in Guatemala belong to different sections. The species with reduced decussate leaves on dorsiventral branchlets (sect. *Complanata*) are often referred to a separate genus, *Diphasiastrum* (earlier to *Diphasium* in error). The remaining six sections seem equally distinct.

- a. Branchlets of aerial shoots not flattened; leaves of branchlets uniform, radially arranged in numerous ranks, lance-linear, hair-tipped. *L. clavatum*.
- a. Branchlets of aerial shoots dorsiventrally flattened, with decussate, scalelike, dimorphic or trimorphic leaves in 4 ranks, without hair tips. *L. thyoides*.

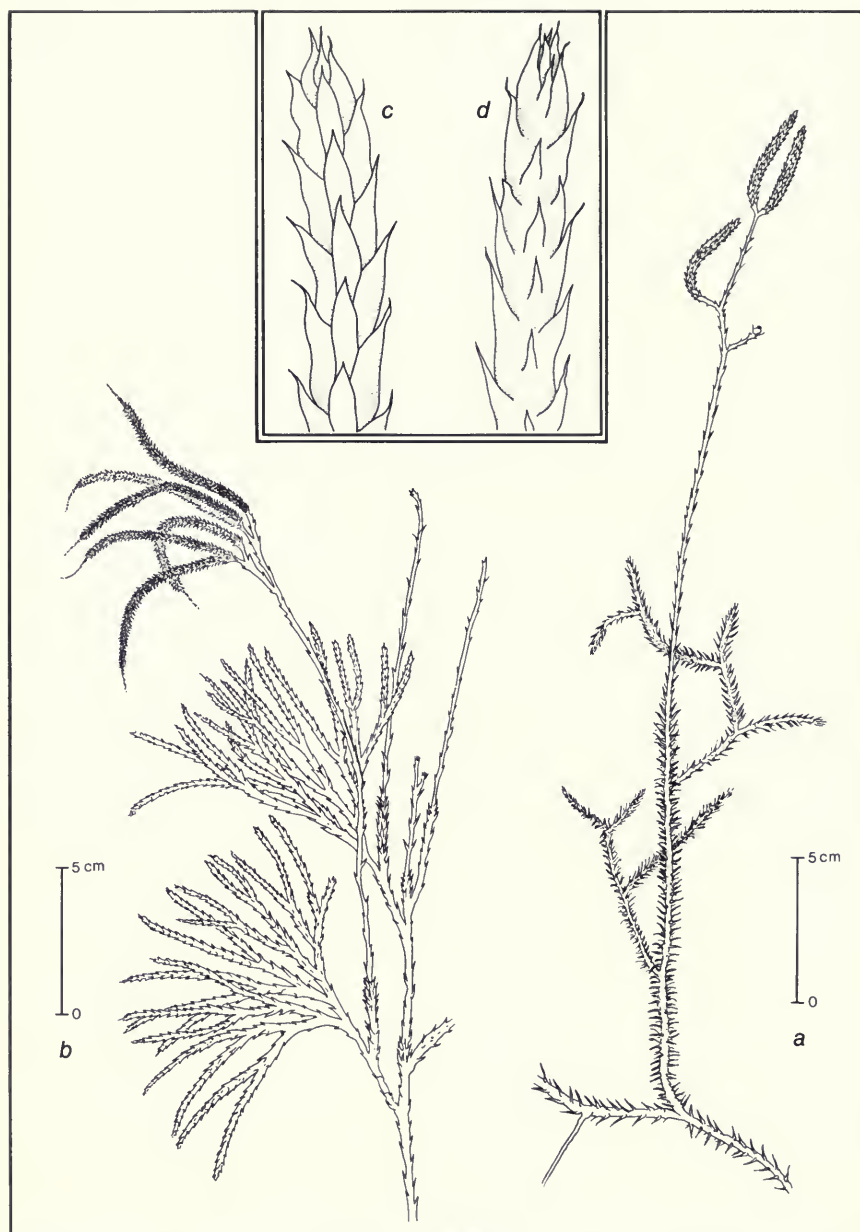


FIG. 7. *Lycopodium* subgenus *Lycopodium*. a, *L. clavatum*, aerial shoot, habit, $\times \frac{1}{2}$. b-d, *L. thyoides*: b, aerial shoot, habit, $\times \frac{1}{2}$; c, tip of branchlet, upper side, $\times 6$; d, tip of branchlet, lower side, $\times 6$.

Lycopodium clavatum L., Species Plantarum 1101. 1753. *Lepidotis clavata* (L.) Pal.-Beauv., Prodrôme Aethéogamie 108. 1805. *Lycopodium aristatum* Humb. & Bonpl. ex Willd., in L., Species Plantarum, ed. 4, 5: 17. 1810. *Lycopodium piliferum* Raddi, Plantarum Brasiliensium 1: 79, t. 3. 1825. *L. trichophyllum* Desv., Mém. Soc. Linn. Paris 6: 134. 1827 (as *trychophyllum*). *L. aristatum* var. *incurvum* Grev. & Hook., Bot. Misc. 2: 376. 1831. *L. aristatum* var. *robustius* Grev. & Hook., loc. cit. *L. clavatum* var. *raddianum* Spring, Flora 21(1): 172. 1838. *L. clavatum* var. *aristatum* (Humb. & Bonpl. ex Willd.) Spring, tom. cit. 173. *L. clavatum* var. *desvauxianum* Spring, loc. cit. *L. clavatum* var. *jamaicense* Spring, tom. cit. 174. *L. aristatum* var. *desvauxianum* Spring, in Martius, Flora Brasiliensis 1(2): 114. 1840. *L. trichiatum* Bory var. *desvauxianum* Spring, Monographie des Lycopodiacees 1: 92. 1842. *L. eriostrachys* Fée, Cryptogames Vasculaires Brésil 1: 224. 1869. *L. clavatum* var. *minarum* Christ, in Schwacke, Plantas Novas Mineiras 2: 41. 1900. *L. clavatum* var. *eriostrachys* (Fée) Nessel & Hoehne, Arch. Bot. São Paulo 1: 435. 1927. *L. clavatum* var. *piliferum* (Raddi) Nessel & Hoehne, loc. cit. *L. clavatum* var. *equisetoides* Schwacke ex Nessel & Hoehne, tom. cit. 438. *L. clavatum* var. *trichophyllum* (Desv.) Nessel & Hoehne, tom. cit. 436. *Bejuca de la mar* (Jalapa, fide Steyermark), *bejuco de pino* (Zacapa, fide Steyermark), *disciplina* (Huehuetenango, fide Steyermark), *kam chax* (vine pine) or *kamcha* (Alta Verapaz, fide M. R. Wilson, P. C. Standley).

In moist to wet montane forests, most collections are from *Pinus-Quercus*, or *Pinus-Liquidambar* forest, trailing over banks, or in moist open areas, and forest edges, 1,300–3,350 m; Alta Verapaz; Baja Verapaz; Chiquimula; Huehuetenango; Jalapa; El Progreso; El Quiché; San Marcos; Zacapa. Humid temperate and boreal regions of the northern hemisphere, montane in the tropics of the Old and New World.

Plants terrestrial, creeping, trailing, or hanging over banks; main stem usually superficial, rooting with long intervals, 2–3 (–4) mm thick excluding leaves; aerial shoot systems arising in a dorsolateral position on the main stem, ascending to stiffly erect, up to at least 50 cm high, repeatedly unequally branched, with strongly diverging to almost parallel branchlets; ultimate branchlets terete, with leaves in spirals, or in irregular alternating whorls of 6–8 (–10), forming 12–16 (–20) indistinct longitudinal ranks, leaves patent to ascending or somewhat imbricate, lance-linear, 6–8 (–10) mm long, 0.5–0.8 mm broad at the base, terminating in a long colorless hair, with smooth to sparsely denticulate margins; peduncles terminating main branchlets, erect, up to 30 cm long, simple, or bearing up to 6 pedicellate strobili; peduncle leaves distant, appressed, reduced in length, partially scarious; strobili 1.5–6 (–8) cm long, ca. 6 mm in diameter including sporophylls, sometimes forked; sporophylls in alternating whorls of 5 or 6, forming 10–12 longitudinal ranks, 4–6 mm long, 1.5–2.2 mm broad, subpeltate, with triangular-ovate to rhombic-ovate acuminate exterior face, with usually broadly scarious, dentate to erose-laciniate margins, the basiscopic sporophyll part often distinct at maturity; sporangia reniform, 1.3–1.6 mm broad.

Lycopodium clavatum is a variable species. Its habit appears to be highly adaptive to external factors, but genetic variation also may be involved. There is an almost continuous series of forms from amply branched plants with diverging branches, spreading, soft-herbaceous leaves, and long, branched peduncles, growing in warm, moist, and sheltered habitats, to small, compact, parallel-branched plants with more imbricate and firm leaves, and short, simple or once-forked peduncles, belonging to cold, exposed habitats. The latter forms in Guatemala approach the Andean *L. contiguum* Klotzsch, which is best considered a subspecies of *L. clavatum*. However, the Guatemalan plants are not so extremely reduced in habit.

A. J. Sharp 451036 (US) is a mixed collection, containing both typical *L. clavatum*

and a plant similar to *L. contiguum*. Other collections from the same area (Santa Eulalia, prov. Huehuetenango) indicate a forest environment which is an unlikely habitat for *L. contiguum*. Further investigation in the area is needed in order to clarify if the plant in question is an odd extreme aberrant, or if it can be taken as a considerable range extension for *L. contiguum*.

Used for altar and fiesta decorations.

Lycopodium thyoides H. & B. ex Willd., in L., *Species Plantarum*, ed. 4, 5: 18. 1810. *L. complanatum* L. var. *tropicum* Spring, in Martius, *Flora Brasiliensis* 1: 116. 1840. *L. complanatum* L. var. *adpressifolium* Spring, *Monographie Lycopodiaceés* 1: 102. 1842. *L. complanatum* L. var. *thyoides* (H. & B. ex Willd.) Christ, in Schwacke, *Plantas Novas Mineiras* 2: 42. 1900 (as *thuoides*). *L. complanatum* L. var. *validum* Weath., *Proc. Amer. Acad. Arts* 45: 414. 1910. *Diphasiastrum thyoides* (H. & B. ex Willd.) Holub, *Preslia* 47: 108. 1975. *Disciplina* (Huehuetenango, *fide* Steyermark).

Terrestrial in moist to wet montane forest, trailing over banks, or in forest edges; most collections are from *Pinus-Quercus* or from *Liquidambar-Pinus* forests, 1,300–3,500 m; Alta Verapaz; Baja Verapaz; Huehuetenango; Jalapa; El Progreso; El Quiché; San Marcos; Zacapa. Greater Antilles; southern Mexico to Panama; montane in South America to northernmost Argentina and southeastern Brazil.

Plants terrestrial; rhizome creeping, trailing, or hanging over banks, superficial, rooting with irregular intervals, terete, 1.5–2.5 mm in diameter excluding leaves; rhizome leaves relatively distant, in irregular spirals, or subverticillate, subulate, appressed to ascending, 2–3 mm long; aerial shoots arising from the rhizomes in a dorsolateral position with irregular intervals, ascending to erect, 10–50 cm high, with vegetative portions up to ca. 30 cm high; the main upright axis terete to somewhat flattened, bearing lateral, flattened, fan-shaped branch systems; ultimate branchlets flattened, dorsiventral, 1.5–4 mm broad including leaves, with trimorphic leaves in 4 ranks, decussate; upper leaves each with a pointed, subulate to acicular, appressed free blade 1–2 mm long, and a conspicuous, ca. 0.4–0.6 mm broad, decurrent base; lateral leaves bilaterally compressed, long-decurrent, 2.5–7 mm long including the bases, the free blades 1–3 mm long, appressed to spreading, acuminate to long-pointed, the leaf bases 0.6–1.5 mm broad, with almost parallel to distinctly diverging margins, often curved down; ventral leaves inconspicuous, acicular, without decurrent base, 1–2 mm long; peduncles terminating main upright axes or stronger axes of upper lateral branch systems, 10–25 cm long, terete, with rather distant, subulate, spirally arranged leaves, each bearing 4–9 pedicellate strobili; strobili 2–8 cm long, 2–3 mm in diameter, often with protracted sterile tips; sporophylls subpeltate, usually in 6 ranks, ca. 2–3 mm long, 1.5–2 mm broad, the outer portion broadly deltoid-ovate, long-cuspidate, with almost entire, broadly scarious margins; sporangia sessile on the sporophyll base, reniform, ca. 1.5 mm broad, with equal valves.

Lycopodium thyoides is easily distinguished from all other species of this genus in the area by its pseudomonopodial branching, and dorsiventral branchlets with decussate leaves, reminiscent of Cypress shoots.

The present application of the name *L. thyoides* is in accordance with the "*L. thyoides*-complex" of Wilce (Beih. Nova Hedwigia 19: 155–158. 1965).

No attempts have been made here to recognize formally the variation encountered in the area. The Guatemalan specimens of *L. thyoides* suggest the existence of perhaps two taxa, differing in the degree of branching and in branchlet width, but formal recognition is better postponed until the entire complex has been carefully revised.

LYCOPODIUM subg. **SELAGO** Baker, *Handbook of the Fern-Allies* 8. 1887. *Huperzia Bernhardi*, J. Bot. (Schrader) 1800(2): 126. 1802. *Plananthus* Pal.-Beauv. ex

Mirbel, in Lam. & Mirbel, Hist. Nat. Vég. 3: 476; 4: 310. 1802. *Lycopodium* subg. *Urostachya* Pritzel, in Engler & Prantl, Die Natürlichen Pflanzenfamilien 1(4): 592. 1900. *Urostachys* (Pritzel) Herter, Beih. Bot. Centralbl. 39: 249. 1922.

Plants epiphytic or terrestrial, with equal dichotomies throughout, the branches all similarly developed or with a slight functional differentiation, pendent, erect, or ascending; roots emerging as a basal tuft; sporophylls and vegetative leaves alike, or sometimes the sporophylls reduced in size, but never subpeltate; sporangia reniform, short-stalked, in the leaf axils; sporangium wall cells sinuate, strongly lignified except on outer surface; spores pitted or grooved; gametophytes subterranean, saprophytic, with filamentous paraphyses.

Subgenus *Selago* is the largest subgenus, with probably more than 300 species. It stands apart from the two other subgenera in several important characters. It seems far more distantly related to these than these are mutually interrelated. Therefore, some authors accept this group as a separate family, Huperziaceae.

The taxonomic problems of the group are great. In contrast to the other subgenera, no useable subdivision is apparent in subg. *Selago*. Groups of various rank have been proposed, but almost all of these seem rather intimately interconnected morphologically. A group of epiphytic species has been separated as the genus *Phlegmariurus* Holub (equivalent of sect. *Phlegmaria* Baker ex Pritzel), mainly on the basis of differences of chromosome base numbers. Although highly suggestive, this evidence comes from very few species and is somewhat ambiguous.

Members of this group inhabit almost all humid regions of the world, from the Arctic to the Antarctic islands and from sea level to the snow limit on mountains. About half of the species are Tropical American with particular diversity along the Andes. Nineteen species are recognized in Guatemala.

- a. Shoots abruptly dimorphic; the sporangiate terminal divisions with strongly reduced, imbricate leaves in 4 ranks; the basal divisions with expanded, spreading, decussate or subdecussate leaves.
 - b. Leaves of sporangiate divisions highly variable, often recurrent to expanded or semiexpanded shape, the shortest sporophylls 2 mm long or longer; expanded leaves ovate to broadly lanceolate, acute. *L. myrsinites*.
 - b. Leaves of sporangiate divisions usually uniform, all appressed, or rarely recurrent to expanded shape; shortest sporophylls 1.5 mm or shorter; expanded leaves lanceolate or elliptic and obtuse.
 - c. Expanded leaves lanceolate, stems usually red or reddish; sporangiate constricted divisions usually 15–25 cm long, with almost uniform sterile and sporangiate leaves. *L. amentacum*.
 - c. Expanded leaves elliptic, obtuse and mucronulate; stems greenish; sporangiate constricted divisions usually less than 10 cm long, their sterile leaves usually longer than sporangiate ones. *L. dichaeoides*.
- a. Leaves uniform throughout, or gradually reduced upward, not decussate or subdecussate, sporophylls in 5 or more ranks.
 - d. Plants erect, or erect from a decumbent to ascending base, epiphytic or terrestrial; leaves rarely twisted at the base to a vertical position (*L. pithyoides* rarely pendent with age).
 - e. Leaf margins somewhat denticulate, leaves spreading to reflexed, less than 10 mm long. *L. reflexum*.
 - e. Leaf margins entire.
 - f. Shoots fingerlike, with thick, imbricate leaves; leaf bases strongly convex and with a basal swelling (air cavity) abaxially. *L. crassum*.
 - f. Shoots with spreading, linear or lanceolate leaves, without basal air cavity.
 - g. Shoots bottlebrush-like, at least in basal divisions; leaves linear, the longest more than 13 mm long; stems 3 mm or more thick excluding leaves.
 - h. Longest leaves 20–35 mm (or more) long, bisulcate above when dry, the vein and margins prominently tumid, the margins somewhat revolute. *L. pithyoides*.

- h. Longest leaves 13–19 mm long, flat or shallowly canaliculate above, the vein sometimes slightly prominent above near the leaf base.
L. mexicanum.
- g. Smaller, not densely leafy plants; leaves narrowly lanceolate, with a narrowed lamina base, the longest 7–11 mm long, stems 1.5–2 mm thick at the base excluding leaves. *L. bradeorum*.
- d. Plants pendulous or initially erect, but recurved to pendulous when fully developed, usually epiphytic; leaves often twisted at the base and the lamina accordingly vertical.
 - i. Vegetative leaves of basal divisions filiform, linear, or lanceolate; the broadest divisions more than 15 mm in diameter including leaves; the longest leaves 10 mm or longer or, if shorter, not acicular or subulate.
 - j. Stems ca. 1 mm or less thick at the base excluding leaves, these not filiform, but broadened in the middle; leaves not arranged in whorls, with a narrowed, sometimes petiole-like, lamina base in the basal leaves; stems greenish white to brown, or red.
 - k. Stems greenish, or brownish when dry; average of longest leaves more than 13 mm; average of broadest leaves 1.5 mm or more. *L. linifolium*.
 - k. Stems red; average of longest leaves 7–10 mm; average of broadest leaves 1 mm or less. *L. capillare*.
 - j. Stems ca. 2 mm or more thick at the base excluding leaves, or ca. 1.5 mm, but then with filiform leaves; leaves more or less regularly whorled or in low, separate spirals, lamina bases narrowed or not.
 - l. Leaves lanceolate, the broadest ones (sometimes only few at the base) more than 1.5 mm broad.
 - m. Leaves, especially of densely sporangiate divisions, ascending to imbricate; lamina bases of vegetative leaves not strongly narrowed and petiole-like.
 - n. Leaves of apical divisions in 10 (or 12) ranks, formed by alternating whorls of 5 (or 6), hardly different from the basal leaves, almost completely concealing the stem and sporangia. *L. cuernavacense*.
 - n. Leaves of apical divisions in 8 or 6 ranks, formed by alternating whorls of 4 or 3, slightly to strongly reduced, the sporangia concealed or readily seen.
 - o. Leaves of apical, densely sporangiate divisions in alternating whorls of 3, forming 6 often very distinct ranks, loosely ascending to imbricate, soft-herbaceous to somewhat coriaceous, usually not concealing the sporangia, often greatly reduced. ... *L. taxifolium*.
 - o. Leaves of apical divisions in alternating whorls of 4, forming 8 ranks, rigidly coriaceous, closely imbricate, covering the stem and sporangia almost completely. *L. hartwegianum*.
 - m. Leaves, even of densely sporangiate divisions, wide-spreading to patent-ascending, often subsecund, the lamina base, at least in basal divisions, narrowed and somewhat petiole-like. *L. orizabae*.
 - l. Leaves linear or filiform, the broadest ones 1 mm broad or less.
 - p. Leaves linear-subulate, 0.7–1 mm broad in the middle, the leaf base without red color. *L. dichotomum*.
 - p. Leaves narrowly linear to filiform, less than 0.5 mm broad in the middle, often with a red dot on the leaf base. *L. wilsonii*.
 - i. Vegetative leaves of basal divisions acicular to subulate, the longest leaves rarely exceeding 6 mm, the broadest divisions rarely exceeding 6 mm in diameter.
 - q. Leaves distinctly modified in size, direction, and shape from the base to the stem apices, sporophylls usually 1–3 mm long and 0.8–1.2 mm broad.
 - r. Shortest sporophylls 2–3 mm long, usually long-acuminate, subcoriaceous, shining, usually not sharply carinate except in the leaf base. ... *L. pringlei*.
 - r. Shortest sporophylls 1–1.5 mm long, acute to short-acuminate, usually soft-herbaceous, dull, abaxially rounded to sharply carinate to the leaf apex.
L. tuerckheimii.
 - q. Leaves almost uniform in direction and shape, but slightly shorter toward stem apices, sporophylls usually 3–4 mm long and 0.5–0.7 mm broad.
L. acerosum.

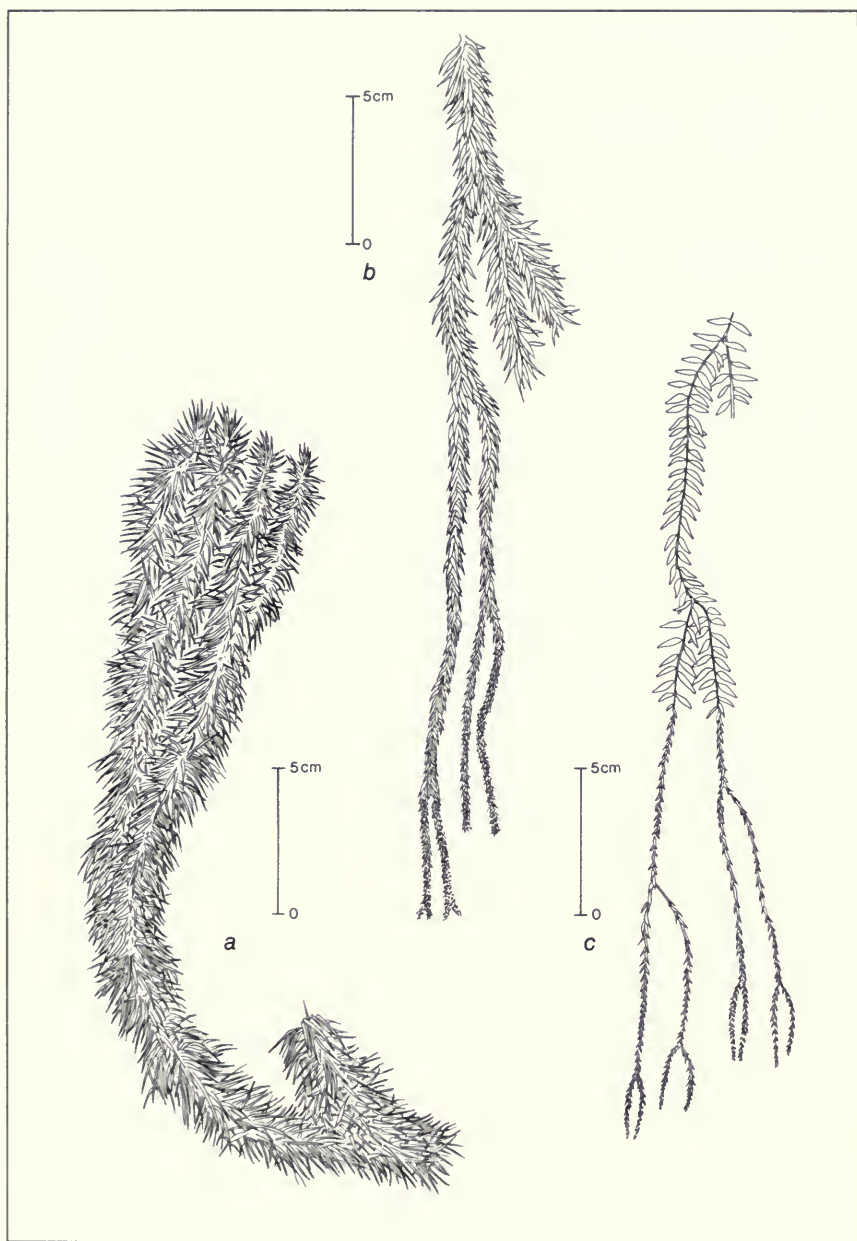


FIG. 8. *Lycopodium* subgenus *Selago*. a, *L. mexicanum*, habit, $\times \frac{1}{2}$. b, *L. taxifolium*, habit, $\times \frac{1}{2}$. c, *L. myrsinites*, habit, $\times \frac{1}{2}$.

Lycopodium acerosum Sw., Flora Indiae Occidentalis 3: 1575. 1806. (lectotype [fide Proctor, p. 25, 1977]: Plumier, *Traité Fougères*, t. 166, fig. B, specimen in Herb. Suriani no. 635 [P]). *Urostachys acerosus* (Sw.) Herter ex Nessel & Hoehne, Arch. Bot. São Paulo 1: 399. 1927. *Disciplina* (Huehuetenango, fide Steyermark).

Epiphytic in lower montane forest, 900–1,500 m; Alta Verapaz; Huehuetenango. West Indies; southern Central America, northern South America (rare); southeastern Brazil.

Plants epiphytic, delicate, flaccidly pendent, at least up to 60 cm long; shoots including leaves almost equally thick throughout, 5–7 mm in diameter, or gradually tapering to 3–4 mm in apical divisions, amply branched, up to 7–10 times dichotomous, with parallel hanging divisions, or the basal ones somewhat spreading, often discontinuously and usually unilaterally sporangiate from 20–30 cm above the base and upward; stems excluding leaves 0.5–0.7 mm thick, tapering to ca. 0.3 mm, usually almost concealed by the leaves, pale green to stramineous; leaves almost uniform throughout or somewhat shorter upward, in the basal divisions borne in alternating whorls, or low, irregular spirals of 5 or 6, forming 10 or 12 indistinct longitudinal ranks, in apical divisions usually with (3–) 4 (–5) leaves in each whorl, densely crowded, the distance between whorls ca. 0.5–1 mm; leaves falcately ascending to sigmoid, upward more imbricate or somewhat secund, linear-attenuate to almost filiform in the basal divisions, 4–6 mm long, 0.2–0.3 mm broad at the base, convex beneath, with decurrent bases, canaliculate above, with smooth margins, soft-herbaceous in texture; vegetative leaves of sporangiate divisions conform, but usually 3–4 mm long; sporophylls with broadened, somewhat clasping base, long-acuminate, 3–4 mm long, 0.5–0.7 mm broad at the base, with a prominent decurrent vein in the base, partly concealing the sporangium; sporangia reniform, ca. 0.7 mm broad.

The present species has commonly been referred to *Lycopodium verticillatum* L. f. or *L. setaceum* Lam., both of which are based on material from Réunion Island and are probably conspecific. In contrast to Proctor (Flora of the Lesser Antilles, 1977, p. 25), I believe that the Tropical American population of the present species is sufficiently distinct from Old World *L. verticillatum* to be maintained as a different species, although they seem close. The Réunion population is more robust and usually more densely and omnilaterally sporangiate and has longer leaves than the American one. *Lycopodium portoricense* Underw. & Lloyd (type from Puerto Rico) is possibly conspecific with *L. acerosum*. It may represent only a luxuriant growth form, growing on soil in ample light.

In Guatemala, *L. acerosum* is most closely related to *L. pringlei* and *L. tuerckheimii*. It is known from only two collections.

Lycopodium amentaceum B. Øllgaard, Amer. Fern J. 72: 53, f. 1–4. 1982.

Epiphytic in montane or cloud forest, 1,800–2,300 m; Guatemala; El Quiché. Colombia; Venezuela.

Plants epiphytic, pendent, up to 60 cm long; shoots with abruptly dimorphic leaves; basal divisions with expanded leaves up to 50 cm long, (10–) 12–20 mm broad including leaves; apical constricted divisions up to 30 cm long, highly compound, tassel-like, 1.2–1.8 mm thick including the imbricate, reduced leaves; stems excluding leaves slender, lax, ca. 1 mm thick at the base, tapering to ca. 0.5 mm upward, terete to somewhat ridged by decurrent leaf bases, usually bright red, up to 6 times dichotomous; expanded leaves of basal divisions decussate or subdecussate, in 4 ranks, with the leaf pairs 2.5–4 mm apart, patent to perpendicular to the stem, oblong-lanceolate, with obtuse or mucronulate apex, with almost symmetric base and apex, straight or somewhat recurved, the lamina usually vertical by a twist of the base; fully expanded leaves (4–) 6–10 mm long, 2–3 (–3.5) mm broad, soft-herbaceous, flat, or slightly folded down along the vein when dry, the vein

evident but not prominent; reduced leaves of apical divisions decussate, the leaf pairs 1–3 mm apart, loosely to closely imbricate, almost uniform throughout, broadly ovate with rounded to acute or mucronate, falcate apex, clasping with the base, abaxially rounded to carinate, 1.2–1.7 mm long, 1.2–1.5 mm broad, equalling or slightly exceeding the sporangia; sporangia ca. 1 mm broad.

Lycopodium amentaceum is a close relative of *L. callitrichifolium* Mett. and *L. cu-neifolium* Hieron., a group of rather rare, delicate epiphytes from the northern Andes and southern Central America. It is distinguished from both of these related species by its larger size, longer, transverse-symmetric, oblong-lanceolate expanded leaves. From *L. myrsinites* it may be separated by the red stems, uniform leaves of the constricted branches, and narrower expanded leaves.

Lycopodium bradeorum Christ, Repert. Spec. Nov. Regni Veg. 8: 20. 1910. *Urostachys bradeorum* (Christ) Herter ex Nessel, Bärlappgewächse 154. 1939 (as *bradeorus*).

Epiphyte in mid-altitude forests, altitude ca. 900 m; Alta Verapaz. Costa Rica; Ecuador.

Plants epiphytic, upright or ascending, bushy, with branches dense and spreading, firm, up to 18 cm high; shoots including leaves usually almost equally thick throughout, ca. 15–20 mm in diameter, 4–8 times dichotomous, sporangiate from ca. 10 cm above the base and upward; stems excluding leaves ca. 1.5–2 mm thick at the base, tapering to ca. 0.7 mm, prominently ridged by decurrent leaf bases, pale brownish when dry; leaves almost uniform in size and shape throughout, not covering the stem, borne in alternating whorls or low spirals of 3, producing 6 indistinct longitudinal ranks, the distance between whorls ca. 1–3 mm; leaves patent-spreading to ascending, straight or slightly recurved, without a basal twist, narrowly lanceolate with a narrowed, petiole-like lamina base and short-acute apex, 7–11 mm long, ca. 1 mm broad, coriaceous, adaxially flat or slightly concave, with revolute smooth margins; the narrowed lamina base of sporangiate leaves usually broadened and somewhat clasping the sporangium; the vein prominent below, forming a prominent decurrent ridge on the stem; leaf bases in basal divisions with broadening and prominently decurrent leaf margins and vein; sporangia reniform, ca. 1 mm broad.

Lycopodium bradeorum is closely allied to *L. orizabae*, which see for discussion. *Lycopodium bradeorum* was reported for the Chiapas province in Mexico by A. R. Smith (1981). However, all specimens cited as such (*loc. cit.* p. 252) were found to fit better into *L. orizabae*.

Lycopodium capillare Sod., Recensio Cryptogamarum Vascularium Quintensium 90. 1883. *L. sarmentosum* Spring var. *rubescens* Spring, Monographie des Lycopodiacees 2: 13. 1850. *L. sarmentosum* var. *capillare* (Sod.) Sod., Anales Univ. Centr. Ecuador XII (81): 328. 1895. *L. guatemalense* Maxon, Contr. U.S. Natl. Herb. 17: 177, pl. 9. 1913 (type from Pansamalá, Tuerckheim ed. Donn.-Sm. 957). *Urostachys guatemalensis* (Maxon) Herter, Repert. Spec. Nov. Regni Veg. 19: 165. 1923. *U. capillaris* (Sod.) Herter, Index Lycopodiorum 54. 1949. *U. rubescens* (Spring) Herter, *tom. cit.* 79.

Epiphytic, in lower montane rain forests, 850–1,500 m; Alta Verapaz; Huehuetenango. Southern Mexico to Costa Rica; northern South America (rare).

Delicate, pendulous epiphytes, 10–34 cm long; stems slender to almost threadlike, 0.5–0.8 mm thick at the base excluding leaves when dry, almost equally thick throughout, straight to slightly flexuous, terete or somewhat ridged by decurrent leaf bases, pale to

bright red, 6–9 (–13) times dichotomous, often with densely aggregated terminal branches, hanging nearly parallel; shoots including leaves almost equally thick throughout, ca. 12–18 mm in diameter, discontinuously sporangiate from 5–25 cm above the rooting base; leaves almost uniform throughout, not whorled, but often in occasional pairs or groups of 3 close together, borne spirally in 4–6 indistinct ranks, subdistant, with an average leaf distance of 1–1.5 mm in sterile zones, often closer in densely sporangiate zones; leaves wide-spreading to obliquely falcate-ascending, their laminae radial-vertical by a twist of the leaf base, narrowly to linear-lanceolate, sometimes almost straight, but usually more or less strongly and obliquely falcate, (5–) 7–10 (–12) mm long, 0.6–1 mm broad, softly to firmly herbaceous, with smooth, flat or slightly revolute margins, the vein obscure to somewhat prominent above; the leaf bases narrowed, petiole-like, perpendicular to deflexed from the stem; sporangia reniform, ca. 1 mm broad.

Lycopodium capillare is related to *L. linifolium*, but can be distinguished from the latter by its more delicate habit and its red stems. *Lycopodium underwoodianum* Maxon (type from Costa Rica) is equally, or even more, delicate, but it has longer leaves and lacks the red color. I am uncertain about its distinctness from *L. capillare*. *Lycopodium underwoodianum* occurs very rarely within the range of *L. capillare*.

Lycopodium crassum H. & B. ex Willd., in L., *Species Plantarum*, ed. 4, 5: 50. 1810. *Urostachys crassus* (H. & B. ex Willd.) Herter ex Nessel, *Bärlappgewächse* 75. 1939. *Huperzia crassa* (H. & B. ex Willd.) Rothmaler, *Feddes Repert Spec. Nov. Regni Veg.* 54: 60. 1944.

In open alpine meadows, 2,700–3,300 m; Huehuetenango. Southern Mexico to Panama; Andean South America south to Peru.

Plants terrestrial, ascending to erect, fully outgrown individuals forming loose clumps with numerous finger-like shoots in the center, and prostrate-ascending, juvenating divisions in the basal periphery; young individuals with few erect shoots from the prostrate basal divisions; erect shoots 6–20 cm high, 1–3 (–4) times dichotomous throughout their length; basal shoots repeatedly branching, giving off erect, and new prostrate, stem apices; shoots terete, equally thick throughout, 6–8 (–10) mm thick including the leaves, 2–3 mm excluding leaves when dry, sporangiate from a few centimeters above the base; leaves in 8 or 10 ranks, formed by alternating irregular whorls of 4–5 leaves, usually imbricate and covering the stem throughout, sometimes ascending to loosely imbricate in basal divisions; vegetative leaves of basal divisions narrowly lanceolate from a 1-mm broad base, convex abaxially, 6–8 mm long, 1–1.3 (–1.5) mm broad, broadest in the middle, upward gradually changing to narrowly triangular-lanceolate, falcately curved, strongly convex, with a prominent basal swelling (air cavity) abaxially, 5.5–6.5 (–8) mm long, 1.3–1.5 mm broad just above junction with stem, evenly tapering, the margins smooth to slightly and irregularly rugulose at the tips, green to yellowish green, usually whitish pruinose; sporangia ca. 1.5–2 mm broad.

The plants referred to this species here are more slender and less colored than the type variety from Ecuador, and it may deserve recognition as a separate taxon, together with similar material from southern Mexico to Costa Rica and Panama. Until the whole complex has been carefully studied, I prefer to apply the name *L. crassum* tentatively, in a broad sense for the Guatemalan plants. Only nomenclatural synonyms are included above.

This species belongs to a group with its main development in the Andean páramos.

Lycopodium cuernavacense Underw. & Lloyd, *Bull. Torrey Bot. Club* 33: 110. 1906. *Urostachys cuernavacensis* (Underw. & Lloyd) Herter ex Nessel, *Bärlappgewächse* 92. 1939 (as *cuernavensis*).

Hanging epiphyte in montane moist or rain forests, or in evergreen cloud forests, 2,900–4,000 m; El Quiché; San Marcos. Southern Mexico (2,100–3,000 m).

Plants epiphytic, robust, pendulous or recurved from an erect base, 15–50 (–65) cm long; shoots up to 4 (–6) times dichotomous, almost equally thick throughout, or gradually tapering toward the apex, 10–25 mm in diameter, including leaves, at the base, upward tapering to (6–) 9–15 mm, sporangiate from 15–25 cm above the base and upward; stems 3–5 mm thick at the base excluding leaves when dry, tapering to ca. 3 (–2) mm, ridged by decurrent leaf bases, pale brownish or greenish when dry; leaves almost uniform throughout, or gradually reduced in size, borne in alternating whorls of 5 (or 6), forming 10 (or 12) indistinct longitudinal ranks, the whorls inserted with intervals of 1–3 mm, gradually more crowded upward; leaves ascending to imbricate, regularly radial or somewhat twisted and subsecund at base, slightly recurved to ascending near the base, upward ascending to imbricate, almost completely concealing the stem and sporangia, narrowly lanceolate, softly to rigidly coriaceous, dull dark green to somewhat shining, flat, or with slightly revolute, smooth margins; basal leaves usually 10–20 mm long, 1.8–2.2 mm broad, broadest just above the base, upward gradually reduced to ca. (6–) 8–10 mm long and 1.7–2 mm broad, often somewhat clasping the sporangium at the base, the vein usually evident throughout; sporangia reniform, 1.5–2 mm broad.

Lycopodium cuernavacense is a close relative of *L. taxifolium* and *L. hartwegianum*. From *L. taxifolium* it can be distinguished by its more rigid, thicker stems which are almost completely concealed by the leaves. The safest character is the number of leaves in the whorls, as indicated in the key. The two are also very different ecologically. *Lycopodium hartwegianum* differs from *L. cuernavacense* mainly in leaf arrangement and width. The two species are ecologically rather alike and are possibly only marginally distinct.

Lycopodium dichaeoides Maxon, Proc. Biol. Soc. Wash. 18: 231–232. 1905. *Urostachys dichaeoides* (Maxon) Herter ex Nessel, Bärblattgewächse 252. 1939.

Humid forests at ca. 1,000 m altitude; Alta Verapaz (type from near Finca Sepacuite, Cook & Griggs 251). Costa Rica; Panama; Colombia; Ecuador.

Pendent epiphytes, at least up to 60 cm long; shoots dimorphic, in the basal divisions of the plant, up to ca. 25–35 cm from the base, ca. 12–17 mm in diameter including the broad, expanded leaves, then abruptly constricted to 1–2 mm including the imbricate reduced leaves of sporangiate, apical divisions; stems slender, terete, and somewhat ridged by decurrent leaf bases, ca. 1 mm thick excluding leaves, pale greenish, up to 6 times dichotomous; leaves of expanded divisions uniform in position, size, and shape throughout, in 4 regular ranks, decussate, almost continuously overlapping throughout, diverging 65°–80° from the stem, elliptic to oblong, broadest in the middle or just below, 6–9 mm long, 3–4 mm broad, with mucronulate apex, and smooth, slightly revolute margins, the vein obscure above, evident but not prominent below; the lamina turned to vertical position; apical constricted divisions usually 3–8 cm long, their leaves in 4 ranks, \pm regularly decussate, all or almost all sporangiate, appressed and clasping with their bases, ovate to triangular-ovate, short- to long-cuspidate, somewhat involute, sharply carinate, ca. 1.5 (–2.7) mm long, ca. 1 (–1.3) mm broad, equalling the sporangia or up to 1.5 times longer, the distance between successive leaf pairs 0.5–1 (–2.5) mm; sporangia ca. 1 mm in diameter.

Lycopodium dichaeoides is often confused with *L. aqualupianum* Spring, to which it is closely related, and with *L. callitrichifolium*. From the former species it is distinguished by its more obtuse and elliptic (not ovate) leaves, which usually diverge by a more open angle from the stem, and especially by its shorter and more slender constricted shoots. The constricted shoots of *L. dichaeoides* are usually almost completely sporangiate, whereas *L. aqualupianum* has extensive sterile zones. *Lycopodium aqualupianum* seems to be absent from Central America, but occurs throughout the Antilles and in northern Venezuela to western Colombia,

where its distribution overlaps that of *L. dichaeoides*. Both species belong to lower altitude forests. *L. callitrichifolium* Mett. occurs in high-altitude montane forests, typically in cloud forests in the northern Andes. It differs from *L. dichaeoides* by its red stems, by a more irregular leaf arrangement in the expanded shoot portions, and by its smaller and more distant, usually not overlapping, leaves.

Lycopodium dichotomum Jacq., Enumeratio Stirpium Vindobonensi 314. 1762. *Huperzia dichotoma* (Jacq.) Trevis., Atti Soc. Ital. Sci. Nat. 17: 248. 1874. *Lycopodium chamaepeuce* Herter, Bot. Jahrb. Syst. 43, Beibl. 98: 50. 1909. *Urostachys dichotomus* (Jacq.) Herter, Beih. Bot. Centralbl. 39: 249. 1922. *U. chamaepeuce* (Herter) Herter, Repert. Spec. Nov. Regni Veg. 19: 164. 1923.

Epiphytic, or occasionally on the ground, in lowland rain forests, sea level to 300 (–900) m; Alta Verapaz; Izabal; Petén. Florida; West Indies; southern Mexico to Panama; northern South America.

Plants usually epiphytic, pendent or recurved, lax to subrigid, sparsely to densely and spreadingly branched, usually up to 25 cm long; shoots including leaves almost equally thick throughout, or tapering from ca. 2.5–4 cm in diameter at the base to ca. 12–20 mm in apical, densely sporangiate divisions, usually 3–5 (–6) times dichotomous, sporangiate from ca. 10–15 cm above the base and upward; stems excluding leaves 2–3 (–5) mm thick at the base, upward tapering to ca. 1.5–2 mm, ridged by decurrent leaf bases, pale green to brownish when dry; leaves almost uniform throughout, or gradually reduced in size upward, borne in alternating whorls or low spirals of 5 or 6, forming 10 or 12 indistinct longitudinal ranks, the distance between whorls ca. 1–1.5 (–2) mm, usually almost concealing the stem; leaves of basal divisions patent to spreading, usually somewhat falcate, upward more ascending, rarely somewhat reflexed, linear-subulate, gradually tapering, 15–23 mm long, 0.7–1 mm broad, adaxially slightly concave to canaliculate and sometimes with slightly prominent vein, abaxially with slightly to sharply prominent vein, herbaceous to somewhat coriaceous, with smooth, revolute margins; leaves of apical divisions conform, or reduced to 8–15 mm long, and to 0.5 mm broad, often twisted at the base and the lamina accordingly vertical, usually softer and flatter; leaf bases green, long and prominently decurrent, as broad as the lamina, or slightly broadening, with sharply prominent vein; sporangia reniform, ca. 1.5 mm broad.

The Guatemalan material of *L. dichotomum* differs somewhat from West Indian and more southern Central American and South American material of the same species. It has a more robust habit, longer and more coriaceous leaves, with basally prominent vein in the basal divisions. These characters are suggestive of *L. pithyoides*, but the two species are otherwise easy to recognize.

Urostachys mertonii Herter (Repert. Spec. Nov. Regni Veg. 28: 108. 1930), *U. schlechtendalii* Nessel (Revista Sudamer. Bot. 6: 164, t. 11, fig. 51. 1940), and *U. lindeneri* Herter ex Nessel (*loc. cit.* fig. 50) have types from Guatemala and Mexico. Their original descriptions and illustrations indicate that they all belong to the present species, but I have not seen the type specimens.

Lycopodium hartwegianum Spring, Monographie des Lycopodiacees 2: 14. 1850. *Huperzia hartwegiana* (Spring) Trevisan, Atti. Soc. Ital. Sci. Nat. 17: 248. 1874. *L. funckii* Herter, Bot. Jahrb. Syst. 43, Beibl. 98: 44. 1909. *L. caracasicum* Herter, Hedwigia 49: 88. 1909. *Urostachys hartwegianus* (Spring) Herter ex Nessel, Bärlappgewächse 90. 1939. *U. caracasicus* (Herter) Herter ex Nessel, *loc. cit.* *U. funckii* (Herter) Herter ex Nessel, *loc. cit.* *U. maxonii* Herter ex Nessel, Revista Sudamer. Bot. 6: 165. 1940.

On rocks, or epiphytic in montane rain forests or cloud forests, ca. 3,000 m;

Sololá. Southern Mexico to Costa Rica; northern Andes from Venezuela to Ecuador.

Plants epiphytic or rupestral, robust, recurved from an erect base, or entirely pendent, 15–25 (–60) cm long; stems 3–5 mm thick at the base excluding leaves, when dry, tapering to ca. 2 mm toward the apex, somewhat ridged by decurrent leaf veins, pale brownish or greenish when dry, up to 6 times dichotomous; shoots including leaves equally thick throughout in young plants, tapering in fully developed plants, 15–20 mm in diameter at the base, upward tapering to (6–) 8–10 mm, sporangiate from 20–30 cm above the base and upward; leaves almost uniform throughout, or gradually reduced in size upward, borne in alternating whorls of 4, forming 8 longitudinal ranks, the whorls inserted with a distance of 2–4 mm, gradually more crowded upward; leaves ascending to imbricate, regularly radial, or slightly twisted and subsecund near the base, upward almost completely concealing the stem and sporangia, lanceolate, rigidly coriaceous, brightly shining, the basal leaves usually 14–20 mm long, 2.5–3.5 mm broad, broadest shortly above the base, upward gradually reduced to ca. 8 mm long and 2 mm broad, often somewhat clasping with the base, the apical leaf portion slightly convex to slightly concave, the margins smooth; the vein somewhat prominent abaxially at the base, decurrent, apically obscure; sporangia reniform, 2–2.5 mm broad.

A close relative of *L. cuernavacense*, which see for discussion of characters. *Lycopodium hartwegianum* appears to be very rare throughout Central America, but it is more frequent in the Andes. Its growth habit varies greatly as a response to exposure and humidity. In Guatemala, it is recorded from a single collection of Volcán Atitlán and from a garden collection from Guatemala City.

Lycopodium linifolium L., Species Plantarum 2: 1100. 1753. *Huperzia linifolia* (L.) Trevisan, Atti Soc. Ital. Sci. Nat. 17: 248. 1874. *Urostachys linifolius* (L.) Herter, Repert. Spec. Nov. Regni Veg. 19: 165. 1923.

Epiphytic in rain forests, montane rain forests, most common in Alta Verapaz, and rarely in seasonal evergreen forests, from sea level to 1,600 m; Alta Verapaz; Huehuetenango; Izabal; Petén; Quezaltenango; San Marcos; Sololá. West Indies; southern Mexico to Panama; northern South America.

Plants epiphytic, flaccidly pendulous, 10–60 (–80) cm long; stems slender, 0.7–1.0 mm thick at the base excluding leaves when dry, slightly tapering upward, almost straight to somewhat flexuous, terete or somewhat ridged by decurrent leaf bases, whitish green in life, pale brownish when dry, 2–5 (–8) times dichotomous, often densely aggregated in terminal fasciculate clusters, hanging nearly parallel to somewhat divergent; shoots including leaves equally thick throughout, or gradually tapering upward, (2.5–) 3–4 cm in diameter near the stem base, in fully developed individuals usually tapering to 2 or 1.5 cm, rarely to 0.7 cm, discontinuously sporangiate from ca. 10–25 cm above the base, almost continuously sporangiate in terminal clusters; leaves usually gradually reduced in length and width from the base and upward, or almost uniform throughout in juvenile plants, not whorled, borne spirally in 5–6 indistinct ranks, but often in occasional pairs or groups of 3 leaves, subdistant, with an average leaf distance of 1.5–3 mm in sterile divisions, more crowded in densely sporangiate divisions; leaves wide-spreading to obliquely falcate-ascending, their lamina radial-vertical by a twist of the leaf base, lanceolate near the stem base, higher up narrowly lanceolate to linear-lanceolate, rarely almost subulate in strongly reduced terminal branches, almost straight to strongly oblique-falcate, 13–24 mm long, 1.5–3 mm broad, usually broadest in the basal third, upward reduced to (5–) 10–15 mm long and (0.5–) 1–2 mm broad, flat, soft-herbaceous, with smooth margins and clearly visible, slightly prominent vein; leaf base strongly narrowed, petiole-like, perpendicular to deflexed from the stem, twisted; sporangia reniform, 1–1.5 mm broad.

A number of varieties can be recognized in *L. linifolium*, but all Guatemalan specimens studied agree with the type variety.

Slender specimens of *L. taxifolium* are often determined as *L. linifolium*, but they are easily recognized by their whorled leaves and thicker stem bases.

Lycopodium mexicanum Herter, Bot. Jahrb. Syst. 43, Beibl. 98: 49. 1909. *Urostachys mexicanus* (Herter) Herter, Repert. Spec. Nov. Regni Veg. 19: 164. 1923.

Usually epiphytic, but frequently terrestrial on mossy rocks or banks, in montane rain forests, cloud forests, and *Cupressus* forests, 2,000–3,330 m; Baja Verapaz; Chimaltenango; Huehuetenango; El Progreso; El Quiché; Sololá. Greater Antilles; southern Mexico to El Salvador and probably Nicaragua.

Plants epiphytic or terrestrial, erect from a decumbent or even hanging base, usually 15–30 cm high or up to 50 cm long, 2–4 (–5) times dichotomous; stems 3–4.5 mm in diameter excluding leaves at the base, when dry, tapering to 1.5–2.5 mm upward, usually densely covered by decurrent leaf bases; shoots including leaves almost equally thick throughout, (1.5–) 2–3.5 (–4) cm in diameter or slightly tapering upward, usually exhibiting a periodic variation in leaf length along the stem, sporangiate in separate, seasonally produced zones from 10–20 cm above the base, upward often continuously sporangiate; leaves crowded, almost uniform throughout, or exhibiting a repeated periodic variation in length along the stem, in 10 or 12 ranks formed by alternating, irregular whorls of 5 or 6, the distance between successive whorls 1–3 mm; leaves spreading to somewhat reflexed, straight to somewhat recurved, or obliquely curved and somewhat secund, rarely patent-ascending, linear to linear-subulate, the longest leaves 13–19 mm, the shortest (6–) 8–11 (–12) mm long, 0.9–1.1 (–1.3) mm broad, flat to shallowly canaliculate above when dry, with obscure to slightly prominent vein at the base, rounded, or with prominent vein beneath, with smooth, slightly revolute margins; leaf bases with prominently decurrent margins and vein, slightly broadening from the leaf insertion, or equally broad, red to pink or brownish; sporangia reniform, ca. 2 mm broad.

The concept of *L. mexicanum* is not entirely clear, because no type was indicated by Herter, and because Herter (1949) later reduced this name to synonymy under *L. pithyoides*. However, the combination of the original diagnosis, with the material from the area in Mexico indicated with it, points to the present concept of the species. According to this, *L. mexicanum* is both morphologically and ecologically different from *L. pithyoides*, and in some characters, seems intermediate between this and *L. hippurideum*. The bisulcate, adaxial sides of the leaves of *L. pithyoides* are readily distinguishable from the smooth or canaliculate ones of both *L. mexicanum* and *L. hippurideum*, but the distinction between the last two species is more subtle. *Lycopodium mexicanum* usually has a marked seasonally induced variation in leaf length, resulting in regular constrictions along the shoots, whereas the leaf development in *L. hippurideum* is almost completely regular. *Lycopodium mexicanum* is predominantly epiphytic, whereas *L. hippurideum* is terrestrial. Since epiphytic habitats are much more liable to dessication during periods of dryness than are adjacent terrestrial habitats, these differences of leaf development may simply reflect the different effect of seasonal climatic variation. On the other hand, the very slight development, along with the lack of coloration of the leaf bases, in *L. hippurideum* seems sufficient reason, in combination with the different ecological preferences, to treat this separately from *L. mexicanum*.

Smith (1981, p. 254) indicates that *L. mexicanum* is a pendent epiphyte. However, label information from Guatemala says that it grows erect. It may have a hanging base, but the shoot apices are then curved upward.

Lycopodium myrsinites Lam., Encyclopédie Méthodique Botanique 3: 654. 1789. *Plananthus myrsinites* (Lam.) Pal.-Beauv., Prodrôme Aethéogamie 111. 1805.

L. patens Willd. ex Sprengel, *Systema Vegetabilium*, ed. 14, 4: 12. 1827. *Huperzia myrsinites* (Lam.) Trevisan, *Atti Soc. Ital. Sci. Nat.* 17: 249. 1874. *L. roraimense* Underw. & Lloyd, *Bull. Torrey Bot. Club* 33: 115. 1906. *Urostachys myrsinites* (Lam.) Herter, *Repert. Spec. Nov. Regni Veg.* 19: 166. 1923. *L. skutchii* Maxon, *Proc. Biol. Soc. Wash.* 46: 159. 1933 (type from Chichavac, 2,400–2,700 m, *Skutch* 243). *U. patens* (Willd. ex Sprengel) Herter ex Nessel, *Bärlappgewächse* 245. 1939. *U. roraimensis* (Underw. & Lloyd) Herter ex Nessel, *tom. cit.* 246. 1939.

Epiphytic or, rarely, hanging from banks, in montane rain forests and evergreen cloud forests, 1,800–3,000 m. Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; El Progreso; San Marcos; Zacapa. Hispaniola; southern Mexico; Trinidad; northern Venezuela to Ecuador; British Guiana; Mt. Roraima.

Plants epiphytic, pendent, at least up to 65 cm long; shoots dimorphic, usually, but not always, sharply differentiated in all branches; basal divisions (up to ca. 50 cm from the base), ca. 10–18 mm in diameter including the broad expanded leaves; apical divisions abruptly, or often within a short transition, constricted to 1.5–2.5 mm thick including the reduced, imbricate leaves; stem excluding leaves slender, lax, ca. 1 mm thick at the base, tapering to ca. 0.5 mm upward, somewhat ridged by decurrent leaf bases, pale greenish, up to 7 times dichotomous; leaves of basal expanded divisions uniform or variable in position, size and shape, in 4 ranks, more or less regularly decussate, subdistant to densely crowded and overlapping, distance of leaf pairs ca. 1.5–6 mm, diverging 70°–85° from the stem, ovate to lanceolate, acute to slightly acuminate, with rounded bases, when fully expanded 7–10 mm long, 2–3.5 (–4) mm broad, with smooth, usually flat margins, the lamina twisted to vertical position, often curved back; vein obscure above, evident but not prominent below; leaves of constricted divisions highly variable, often with complete reduction series from expanded to clasping and imbricate, and recurrent series to expanded form, continuously or discontinuously sporangiate, decussate or subdecussate; transitional leaves with broadly ovate bases and short to long-acuminate apex, appressed and clasping with the broad bases, abaxially rounded to bluntly carinate, with straight to recurved apex, 2.5–5 mm long, 1.5–2 mm broad; most reduced leaves with conform bases, but short, straight to falcate apex, bluntly to sharply carinate, scarcely exceeding the sporangia, ca. 2 mm long; sporangia 1–1.3 mm broad.

Lycopodium myrsinites is the commonest epiphytic species with abruptly constricted shoots. The other two species with similar habit are rare in Guatemala.

The closest relatives are South American, viz., *L. phyllicifolium* Desv. ex Poir. and *L. subulatum* Desv. ex Poir., both of which have narrower leaves and less labile leaf shape in the apical divisions. Species of the *L. quadrifariatum* Bory alliance from southeastern Brazil were erroneously placed under *L. myrsinites* by several earlier authors.

Lycopodium orizabae Underw. & Lloyd, *Bull. Torrey Bot. Club* 33: 110. 1906. *Urostachys orizabae* (Underw. & Lloyd) Herter ex Nessel, *Bärlappgewächse* 175. 1939.

Epiphytic or occasionally on rocks, in mid- to high-altitude evergreen forests and cloud forests, 900–2,700 (–3,300) m; Alta Verapaz; Chiquimula; Huehuetenango; El Progreso; El Quiché. Southern Mexico.

Hanging or recurved epiphytes, bushy, with branches dense and spreading, lax to somewhat rigid, usually up to 20 (–32) cm long; shoots including leaves usually slightly tapering, from ca. 20–30 mm in diameter at base to ca. 15–20 mm in apical divisions, usually 5–8 times dichotomous, sporangiate from ca. 10–15 cm above the base and upward; stems excluding leaves 2–3 mm thick at the base, upward tapering to ca. 1 mm, prominently ridged by decurrent leaf bases, pale greenish to brownish when dry; leaves almost uniform throughout or somewhat reduced apically, borne in alternating whorls or

low spirals of 3 or 4, forming 6 or 8 indistinct longitudinal ranks, the distance between whorls ca. 2–3 mm, usually not covering the stem, patent to spreading, straight to somewhat falcately ascending, the basal ones rarely somewhat reflexed, often with a basal twist, and the lamina accordingly vertical, narrowly lanceolate, usually with a long narrow tip, with a narrowed, petiole-like lamina base, 13–19 mm long, (1.0–) 1.3–2 mm broad in basal divisions, upward reduced to (8–) 10–15 mm long, 0.7–1 mm broad, soft-herbaceous to somewhat coriaceous, adaxially flat or slightly concave, with somewhat revolute, smooth margins; in densely sporangiate divisions, the narrowed lamina base often somewhat broadened at the stem junction; the vein evident to basally prominent below; decurrent leaf base with prominent broadening margins and vein; sporangia reniform, ca. 1.5 mm broad.

Lycopodium orizabae is most closely related to *L. bradeorum*, from which it is distinguished by its longer, narrower leaf tips, larger, less coriaceous leaves, especially in the basal divisions. Also, *L. bradeorum* is apparently an erect epiphyte, whereas *L. orizabae* is reported to be pendent. The decurrent leaf bases of *L. orizabae*, and also of *L. bradeorum*, are reminiscent of *L. pithyoides*, *L. dichotomum*, or *L. mexicanum*, whereas most other characters resemble *L. linifolium*.

Lycopodium pithyoides Schlecht. & Cham., *Linnaea* 5: 623. 1830. *L. mandiocanum* Raddi var. *mexicanum* Spring, *Monographie des Lycopodiacees* 1: 45. 1842. *L. gigas* Herter, *Bot. Jahrb. Syst.* 43, Beibl. 98: 50. 1909. *Urostachys gigas* (Herter) Herter, *Repert. Spec. Nov. Regni Veg.* 19: 164. 1923. *U. pithyoides* (Schlecht. & Cham.) Herter, *loc. cit.*

Epiphytic, often in oak trees, in lower to mid-altitude montane rain forests, or seasonal evergreen forests, 600–1,200 (–1,600) m; Alta Verapaz; El Progreso. Cuba; southern Mexico; Costa Rica; Venezuela.

Plants epiphytic, erect, or rarely recurved to pendent with age, usually 15–25 cm high, up to 35 cm long, usually 3–4 (–8) times dichotomous, old pendent plants often with densely aggregated terminal clusters of narrow shoots; shoots including leaves equally thick throughout, 4–7 cm in diameter, or tapering to ca. 2 (–1.5) cm in old plants, sporangiate in separate, seasonally produced zones from 10–20 cm above the base and upward or continuously sporangiate in terminal pendent branches; stems 4–6 mm in diameter excluding leaves at the base, when dry, tapering to 2–3 mm upward, usually completely covered by the broad, bright red, decurrent leaf bases; leaves uniform throughout, or gradually reduced in length upward, in 8 or 10 ranks, formed by alternating whorls of 4 or 5, the distance between whorls 1–2.5 mm; leaves spreading to reflexed, usually straight, somewhat coriaceous, sometimes with a basal twist and sidewise falcately ascending in apical divisions, 2–3.5 (–4.5) cm long, in old plants sometimes reduced to 15 (–10) mm, 0.7–1.2 mm broad at the base, tapering in the apical half, bisulcate above when dry, with prominently tumid vein and margins, the vein prominent to sunken beneath; leaf bases with prominently decurrent margins, and a median veinal ridge, broadening to ca. 2 mm, bright red or brownish, at least in the center and the base of the vein; sporangia reniform, ca. 2 mm broad.

The very long, bisulcate leaves and the red stems make the present species easily recognizable, although age implies great variation of habit.

Lycopodium pithyoides is most closely related to *L. mandiocanum* Raddi of southeastern Brazil and Paraguay. From this it is distinguished mainly by its greater dimensions. In Guatemala its closest relative is *L. mexicanum*, under which the relationship is discussed.

Lycopodium pringlei Underw. & Lloyd, *Bull. Torrey Bot. Club* 33: 109. 1906. *L. fontinaloides* Spring var. *mexicanum* Spring, *Monographie des Lycopodiacees* 1: 49. 1842. *Urostachys pringlei* (Underw. & Lloyd) Herter ex Nessel, *Bärlappgewächse*

131. 1939. *Cordelino* (Jalapa, *fide* Steyermark); *disciplina* (Huehuetenango, *fide* Steyermark).

Usually epiphytic, occasionally on wet open banks, in humid montane forests and cloud forests, 1,600–2,700 (–3,200) m; Alta Verapaz; Chimaltenango; Guatemala; Huehuetenango; Jalapa; El Quiché; San Marcos; Zacapa. Southern Mexico.

Plants epiphytic or rupestral, pendulous, or juvenile and rupestral plants often initially ascending with drooping to pendent apices, up to 60 (–80) cm long; shoots including leaves usually gradually tapering from 6 (–10) mm in diameter in basal divisions, to ca. (1–) 2–3 mm in apical divisions, amply branched, usually 4–6 (–8) times dichotomous, flaccid, hanging parallel from initially diverging branchings, usually discontinuously, omnilaterally sporangiate from 10–50 cm above the base and upward; stems excluding leaves 0.7–1.3 mm thick at the base, tapering to ca. 0.5 mm, usually almost concealed by leaves, pale greenish to brownish when dry; leaves gradually modified and reduced from the base to stem apices; leaves of basal divisions in alternating whorls of 4–5, forming 8–10 indistinct ranks, or often in low, irregular, separate spirals, densely crowded, the distance between whorls ca. 1–2.5 mm, ascending, somewhat sigmoid or secund, acicular-subulate, with slightly broadened junction to the stem, 4.5–6 (–7) mm long, 0.5–0.7 mm broad just above the broadened base, abaxially convex or rarely concave, with entire, usually involute, margins, somewhat coriaceous and shining; leaves of apical divisions usually in irregular whorls of 3–4, forming 6–8 ranks, loosely to closely imbricate, ca. 3 mm long, ca. 0.7 mm broad at the base, otherwise conform; sporophylls 2–3 (–4) mm long, ca. 0.8–1.2 mm broad, ovate-lanceolate, short- to long-acuminate, subcoriaceous, usually shining, partly concealing the sporangia; sporangia ca. 1 mm broad.

Lycopodium pringlei is the most robust member of the *L. verticillatum* group in Guatemala. From *L. acerosum* it can be recognized by its longer, broader, thicker and more coriaceous and distant leaves, and by its distinctly modified apical divisions, whereas *L. acerosum* has a uniform, almost feather-like aspect throughout in the Guatemalan specimens I have seen.

The delimitation toward *L. tuerckheimii* is problematic and is mainly a matter of size differences. However, *L. tuerckheimii* usually has more strongly reduced, shorter, soft-herbaceous, dull sporophylls. Also, this species seems confined to a lower altitudinal range than *L. pringlei*.

The type of *L. pringlei* (Pringle 4994, from Oaxaco, Mexico) represents an extreme form with very tightly appressed leaves throughout, a situation which is not matched in any of the Guatemalan specimens studied. The same situation is found in the type of *L. tortile* Christ (Costa Rica) which agrees in most characters, but has only approximately half the size of *L. pringlei*.

***Lycopodium reflexum* Lam.**, Encyclopédie Méthodique Botanique 3: 653. 1789. *Plananthus reflexus* (Lam.) Pal.-Beauv., Prodrôme Aethéogamie 100. 1805. *Huperzia reflexa* (Lam.) Trevis., Atti Soc. Ital. Sci. Nat. 17: 248. 1874. *Urostachys reflexus* (Lam.) Herter, Beih. Bot. Centralbl. 39: 249. 1922 (only nomenclatural synonyms included).

In pioneer vegetation on moist open or shaded banks, in montane forests, rarely epiphytic on tree trunks, or in bogs, (1,000–) 1,200–2,600 (–3,500) m; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; San Marcos; Sololá; Zacapa. West Indies; southern Mexico to Panama; South America.

Plants terrestrial, or occasionally epiphytic, erect or ascending from a decumbent base, 8–27 (–40) cm long, sparsely branched, or up to 5 times dichotomous, the divisions usually

parallel or slightly diverging; stems excluding leaves 1.5–2.5 (–4) mm thick at the base, tapering to ca. 1 mm upward or equally thick throughout, pale greenish to stramineous when dried, somewhat tumid in life; shoots including leaves equally thick throughout, (7–) 10–13 (–15) mm in diameter, sporangiate throughout from 2–10 cm above the ground, or in seasonally produced zones; leaves uniform in size and shape throughout in more or less regular, often oblique, alternating whorls of 6 or 7 (–8) leaves, forming 12–14 (–16) ranks, crowded to somewhat distant, the distance between successive leaf whorls 1–2 mm; leaves spreading or recurved to reflexed, subulate, herbaceous to subcoriaceous, 4.5–8 mm long, 0.5–1 mm broad just above the base, with slightly narrowed junction to the stem, evenly tapering, with denticulate to stiffly ciliate margins, flat, or with a low to prominent and decurrent vein below; sporangia reniform, 0.8–1.5 mm broad.

Lycopodium reflexum is somewhat reminiscent of *L. mexicanum*, but is easily distinguished from the latter by its smaller size, light green color, and denticulate leaf margins.

Lycopodium reflexum is highly varied with respect to direction and crowding of leaves, as well as general size. Also, the length and number of teeth on the leaf margins is variable. It is believed that at least part of this variation is genetically based, but at the same time, a detailed study of the entire species complex is needed in order to provide a useable subdivision of it. Many names, both at species and subspecific rank, have been given to members of the complex, but few of these can be applied with any confidence yet.

In Guatemala, a single collection from an exposed, rocky summit on Volcán Atitlán (*Steyermark* 47485; F) stands apart both in morphology and ecology. By its thick stem (ca. 4 mm excluding leaves), dense branching, and crowded, leathery leaves, it closely resembles the Antillean *L. reflexum* var. *rigidum* (J. F. Gmelin) Proctor.

Lycopodium taxifolium Sw., *Prodromus* 138. 1788. *L. passerinoides* H.B.K., *Nova Genera Species Plantarum* 1: 41. 1816. *L. nitens* Schlecht. & Cham., *Linnaea* 5: 623. 1830. *L. herminieri* Spring, *Bull. Acad. Roy. Sci. Bruxelles* 8: 514. 1841. *Huperzia taxifolia* (Sw.) Trevis., *Atti Soc. Ital. Sci. Nat.* 17: 248. 1874. *H. passerinoides* (H.B.K.) Trevis., *loc. cit.* *L. schwendeneri* Herter, *Bot. Jahrb. Syst.* 43, Beibl. 98: 50. 1909. *Urostachys taxifolius* (Sw.) Herter, *Repert. Spec. Nov. Regni Veg.* 19: 162. 1923. *U. herminieri* (Spring) Herter, *loc. cit.* *U. schwendeneri* (Herter) Herter, *tom. cit.* 165. *U. nitens* (Schlecht. & Cham.) Herter., *tom. cit.* 164. *U. passerinoides* (H.B.K.) Herter ex Nessel & Hoehne, *Arch. Bot. São Paulo* 1: 417. 1927. *U. bruelkei* Nessel, *Repert. Spec. Nov. Regni Veg.* 36: 184, t. 173. 1934. *Phlegmariurus taxifolius* (Sw.) Löve & Löve, *Taxon* 26: 324. 1977.

Pendent or recurved epiphytes in tropical and montane rain forests or cloud forests, 300–1,800 (–2,600?) m; Alta Verapaz; Huehuetenango; Izabal; Zacapa. West Indies; southern Mexico to Panama; northern South America.

Plants epiphytic, lax and pendent, or sometimes recurved from an erect and somewhat rigid stem base, up to 50 (–70) cm long; shoots including leaves usually gradually tapering from ca. 20–30 mm in diameter at the base to (3–) 4–7 mm in distal, densely sporangiate divisions of fully developed plants, sporangiate from 10–50 cm above the base and upward, sometimes not or only slightly tapering (juvenile or tardily sporangiate plants), rarely abruptly constricted; stems excluding leaves 2–3.5 mm thick at the base when dry, tapering to 1–1.5 mm toward the apex, somewhat ridged by decurrent leaf bases, pale greenish or brownish when dry, usually 4–5 (–7) times dichotomous; leaves usually gradually reduced and modified upward, borne in alternating whorls or irregular low spirals of 3 or 4, forming 6 or 8 indistinct longitudinal ranks, the distance between whorls 1.5–4 mm; leaves of basal

divisions spreading to ascending or somewhat appressed, often twisted at the base, and accordingly the lamina vertical, narrowly lanceolate, broadest below the middle or just above the base, broadly joined to the stem, firm, or stiff, 14–23 mm long, 2–2.5 mm broad, almost flat or somewhat concave above, with flat or slightly revolute, smooth margins, the vein evident to somewhat prominent below; leaves of middle and apical divisions gradually shorter, narrower, and more appressed, abaxially more convex, with involute margins; leaves of fully sporangiate divisions often distinctly 6-ranked, with strongly broadened concave base, partly concealing the sporangia, often abruptly contracted into a short to long, narrow, involute apex, 3–8 mm long, 1–1.5 (–2) mm broad; sporangia ca. 1–1.5 mm broad.

For comparison with other related species in Guatemala, see *L. cuernavacense*.

Lycopodium taxifolium is a widespread and polymorphic species in tropical America. However, the Guatemalan population appears rather uniform. The variation can mainly be ascribed to the growth conditions. A few collections tend to intergrade in leaf shape and texture with *L. cuernavacense*, but the number of leaves in the whorls readily separates them.

Lycopodium tuerckheimii Maxon, Contr. U.S. Natl. Herb. 13: 23, pl. 1. 1909. *Urostachys tuerckheimii* (Maxon) Herter, Repert. Spec. Nov. Regni Veg. 19: 163. 1923.

Epiphytic, or rarely on rocks, in forests, 1,300–1,600 m; Alta Verapaz (type from near Cobán, *Tuerckheim II* 1864, Jan. 1908 [US]); Baja Verapaz. Southern Mexico; possibly south to Costa Rica.

Plants epiphytic or rarely rupestral, pendent, up to 45 cm long; shoots including leaves gradually tapering from ca. 4–5 (–6) mm in diameter at the base, to ca. 1–1.5 (–2) mm in apical divisions, amply branched, usually 5–9 times dichotomous, delicate, flaccidly hanging from (initially) often strongly diverging branchings, continuously or discontinuously, unilaterally or omnilaterally sporangiate from 7–30 cm above the base and upward; stems excluding leaves 0.5–1 mm thick at the base, tapering to ca. 0.5 mm upward, almost completely concealed by the leaves, pale greenish to stramineous when dry; leaves gradually modified and reduced from the base to the apices; leaves of basal divisions densely crowded, in ca. 8–10 ranks, ascending to closely imbricate, rarely somewhat secund, acicular-subulate, with slightly broadened junction to the stem and narrowly decurrent bases, abaxially with prominently decurrent vein, 4–5 (–6) mm long, 0.2–0.4 mm broad just above the broadened base, thin to subrigid, abaxially strongly convex, canaliculate above, with involute margins, or rarely abaxially flat to concave; vegetative leaves of apical divisions usually in irregular whorls of 3–4, these 1–2 mm apart, forming 6–8 indistinct ranks, closely imbricate, 2–3 mm long, ca. 0.5 mm broad, usually strongly involute when dried; sporophylls conform or shorter, broadly ovate and acute to lanceolate and long-acuminate, 1–2 (–3) mm long, 0.8–1 mm broad, in ultimate divisions often equalling or scarcely exceeding the sporangia, rounded to carinate abaxially, soft-herbaceous, dull, partly concealing the sporangia; sporangia 0.8–1.2 mm broad.

See *L. pringlei* for comparison with other Guatemalan species.

Lycopodium tortile Christ (type from Costa Rica) is very similar, but differs in longer, more coriaceous sporophylls. In case it is considered conspecific, *L. tortile* has priority over *L. tuerckheimii*.

Lycopodium wilsonii Underw. & Lloyd, Bull. Torrey Bot. Club 33: 111. 1906. *L. trichodendron* Herter, Bot. Jahrb. Syst. 43, Beibl. 98: 49. 1909. *L. stamineum* Maxon, Smithsonian Misc. Collect. 56(29): 2–3. 1912. *Urostachys wilsonii* (Underw. & Lloyd) Herter, Repert. Spec. Nov. Regni Veg. 19: 163. 1923. *U. trichodendron* (Herter) Herter, loc. cit. *L. arcanum* Maxon ex Yuncker, Field Mus. Nat. Hist., Bot. Ser. 17: 310, pl. 3. 1938.

Montane forests, 1,300–1,500 m; Huehuetenango; San Marcos. West Indies; southern Mexico to Panama; Venezuela to Ecuador.

Plants epiphytic, erect or pendent when young, arcuate-spreading to pendulous with age, 10–25 cm long, up to 4 (–5) times dichotomous, the divisions more or less divergent; stems 1.5–2 mm thick excluding leaves at the base, when dry, tapering to ca. 1 mm upward; shoots including leaves equally thick throughout or slightly tapering, 10–25 mm in diameter, sporangiate from ca. 10 cm above the base, first in separate seasonally produced zones, upward continuously sporangiate; leaves crowded, uniform throughout, in 10 or 12 ranks formed by alternating irregular whorls of 5 or 6, the distance between successive whorls 1–2 mm, wide-spreading to ascending, straight to somewhat falcately curved, omilateral to somewhat secund, narrowly linear to almost filiform, 7–15 mm long, 0.4–0.7 mm broad at the base when dry, quickly narrowing to ca. 0.3 mm, tapering outward, adaxially concave to canaliculate when dry, with smooth margins, the vein prominent near the leaf base beneath; leaf base broadening and decurrent, with prominently decurrent vein, sometimes with slight red coloring; sporangia reniform, ca. 1.5 mm broad.

Lycopodium wilsonii is a rare plant in Guatemala, known only from two collections. It is easily recognized by its extremely narrow, hairlike leaves. Its growth habit is variable, partly in correlation with the age of plants, young plants usually being erect with spreading to almost horizontal leaves, later turning over to a recurved or pendent habit with more ascending leaves, but juvenile plants also may be pendent. In habit and aspect, *L. wilsonii* resembles slender forms of *L. dichotomum*, to which it seems related. The occurrence of small red spots at the leaf bases in some specimens of *L. wilsonii* suggests a drop of common blood with *L. pithyoides* and *L. mexicanum*.

SELAGINELLACEAE

Plants heterosporous, small and delicate to moderate-sized and sometimes coarse, terrestrial or epipetric, occasionally epiphytic (but not in ours), creeping, ascending or erect; stems branched, often profusely so, continuous, or articulate, or constricted at or near the nodes and here often discolored, producing elongated, filamentous or wiry rhizophores at or near the base or all along the stem from base to stem apex; leaves numerous, minute, with a single, unbranched vein, monomorphic and spirally arranged, or dimorphic and dorsiventrally arranged, in the latter case the vegetative leaves consisting of 2 rows of smaller, usually appressed, median leaves on the upper plane and 2 rows of larger, spreading, lateral ones on the lower plane; sporophylls commonly somewhat modified, but rarely differentiated into median and lateral kinds, borne at the branch tips in (usually) tetraginous spikes (strobili); a ligule, minute, obscure and soon withering, borne at or near the axil of each leaf; sporangia borne singly in the axils of sporophylls, of two kinds: megasporangia, containing 1–4 megaspores which develop into female gametophytes, or microsporangia, containing numerous microspores which develop into male gametophytes.

The family contains a single genus.

SELAGINELLA Palisot de Beauvois

REFERENCES: A. Spring, *Selaginella*, in Monographie des Lycopodiacees, 2. 1850 (preprint of Mém. Acad. Roy. Sci. Belgique 24: 52–264. 1850). A. H. G. Alston, The heterophyllous *Selaginellae* of continental North America, Bull. Brit. Mus. (Nat. Hist.), Bot. 1(8): 219–274. 1955. R. M. Tryon, *Selaginella rupestris* and its allies, Ann. Missouri Bot. Gard. 42: 1–99. 1955. C. F. Reed, Index *Selaginellarum*, Mem. Soc. Brot. 18: 1–287. 1965–66. A. H. G. Alston et al., The genus *Selaginella* in tropical South America, Bull. Brit. Mus. (Nat. Hist.), Bot. 9: 233–330. 1981.

Characters are those of the family.

Selaginella constitutes a natural and distinctive genus of about 600 species, chiefly occurring in tropical and subtropical regions throughout the world. Many species are cultivated and used as ornamentals and border plants in conservatories, and others have been sought as house plants, particularly a few of the densely caespitose, rosette-type species popularly known as "resurrection ferns" (e.g., *S. convoluta*, *S. pallescens*).

- a. Plants homophyllous throughout, the leaves borne on all sides of the stem and branches and all appressed for most of their length [subg. *Selaginella*]. *S. steyermarkii*.
- a. Plants heterophyllous (at least distally), the vegetative leaves of branches and (often) main stems consisting of 2 rows of smaller, usually appressed, median leaves and 2 rows of larger, spreading, lateral ones [subg. *Stachygynandrum*].
 - b. Stems articulate, or at least constricted at or near the nodes and here often discolored; rhizophores produced from the upper surface of the stem; microspores tawny or beige.
 - c. Median leaves biauriculate at base (although 1 or both auricles often somewhat reduced).
 - d. Median leaves aristate, their bases with very short auricles; all leaves eciliate. *S. silvestris*.
 - d. Median leaves acute or short-acuminate, their bases with at least 1 of the auricles large and conspicuous; all or most leaves ciliate at base. *S. galeottii*.
 - c. Median leaves peltate at base, i.e., a single lobelike projection extending below the point of attachment.
 - e. Axillary and lateral leaves rounded or truncate at base, lobes or auricles essentially lacking; axillary leaves subentire or serrulate at base, or rarely short-ciliate and then the cilia 0.1 mm long or less. *S. sertata*.
 - e. Axillary and lateral leaves (except perhaps in newest growth) cordate to biauriculate or sagittate at base, the axillary leaves with 2 lobes or auricles, lateral leaves with at least 1 basal lobe acute and overlapping the axis; axillary leaves ciliate, the cilia 0.2 mm long.
 - f. Axillary leaves with basal lobes subparallel, contiguous (rarely imbricate); lateral leaves with basal acroscopic lobe usually broadly arching over and directed down along the axis. *S. eurynota*.
 - f. Axillary leaves with basal lobes divergent, auriculate; lateral leaves with basal lobes straight, acute, at least the acroscopic one elongated and touching or overlapping the axis. *S. schizobasis*.
 - b. Stems neither articulate nor with discolored or constricted nodes; rhizophores produced from the lower surface of the stem; microspores orange or reddish (pale orange to tawny in *S. oaxacana*).
 - g. Stems caespitose and/or homophyllous and unbranched in the proximal $\frac{1}{3}$ – $\frac{1}{2}$ of stem (but heterophyllous nearly to base in *S. hoffmannii*).
 - h. Stems densely caespitose or (infrequently) crowded to approximate.
 - i. Stems reddish, at least toward base. *S. pallescens* var. *acutifolia*.
 - i. Stems stramineous to greenish or castaneous.
 - j. Lateral leaves concolorous, becoming tawny in age; median leaves acuminate to aristate, green throughout or, most commonly, with a conspicuous whitish marginal band. *S. pallescens* var. *pallescens*.
 - j. Lateral leaves (more mature ones) castaneous on the acroscopic side; median leaves acute to rostrate, green throughout or occasionally with inconspicuous, narrow, pale margins. *S. convoluta*.
 - h. Stems solitary or remote.
 - k. Stems heterophyllous nearly to base, there commonly pinkish or roseate; median leaves with narrow but conspicuous pale green or whitish band of tissue along margin. *S. hoffmannii*.
 - k. Stems homophyllous throughout the unbranched portion, stramineous to reddish; median leaves with pale marginal band lacking or scarcely discernible.

- l. Stems reddish; median leaves acute or (rarely) acuminate. *S. umbrosa*.
- l. Stems stramineous to pale yellow-green; median leaves aristate.
 - m. Axillary leaves naked or sparsely ciliate at base; lateral leaves mostly truncate or geniculate at base on basiscopic side. *S. oaxacana*.
 - m. Axillary leaves conspicuously ciliate at base; lateral leaves rounded at base on basiscopic side. *S. illecebrosa*.
- g. Stems not caespitose, fully heterophyllous, branching nearly throughout.
 - n. Stems pinkish, at least at base. *S. hoffmannii*.
 - n. Stems never pinkish.
 - o. Median leaves of stems and main branches with 1 or 2 free, rather conspicuous, lobes or auricles at base.
 - p. Median leaves acute (rarely short-acuminate); plants prostrate, mostly rooting throughout. *S. delicatissima*.
 - p. Median leaves mostly aristate (or a few long-acuminate); plants suberect to (occasionally) decumbent, commonly rooting in the proximal half.
 - q. Lateral leaves 1.8–3 mm long; apical awn of median leaf (when present) to $\frac{1}{3}$ the length of rest of leaf; base of median leaf lacking cilia (a few short, stiff setae may be present). *S. stenophylla*.
 - q. Lateral leaves (larger ones) 4–5 (–6) mm long; apical awn of median leaf $\frac{1}{2}$ the length of, to equalling, rest of leaf; base of median leaf commonly long-ciliate. *S. martensii*.
 - o. Median leaves rounded to subcordate at base, or occasionally with a single, inconspicuous lobelike projection and then this fully attached to the axis.
 - r. Margins of median leaves setose or ciliate, at least on one side (often inconspicuous in *S. mollis*).
 - s. Rhizophores filiform, commonly 0.05–0.2 mm thick and 0.5–2 (–3) cm long.
 - t. Median leaves with broad, conspicuous white margins, those of the branches strongly imbricate. *S. reflexa*.
 - t. Median leaves green, or rarely with a pale, scarcely discernible, thin margin, those of the branches well spaced to contiguous.
 - u. Lateral leaves nearly as broad as long; rhizophores less than 0.1 mm thick; mature strobili 1–2 mm long. *S. ovifolia*.
 - u. Lateral leaves commonly 2–3 times longer than broad; rhizophores 0.1–0.2 (–0.3) mm thick; mature strobili (3–) 4–10 mm long. *S. mollis*.
 - s. Rhizophores stout and straight, larger ones 0.3–0.9 mm thick and 4–8 cm long.
 - v. Median leaves (most of them) nearly circular, nearly as broad as long; lateral leaves (at least those of the main stem) spreading at ca. 90° from the axes. *S. idiospora*.
 - v. Median leaves ovate to elliptic, obviously longer than broad; lateral leaves spreading at 30°–60° from the axes.
 - w. Median leaves aristate; lateral leaves ciliate in proximal portion, the length of some cilia $\frac{1}{4}$ – $\frac{1}{2}$ the breadth of the leaf. *S. huehuetenangensis*.
 - w. Median leaves acute to acuminate; lateral leaves setose to ciliate (or rarely 1 or 2 long cilia present at acroscopic base). *S. guatemalensis*.
 - r. Margins of median leaves entire to serrulate.
 - x. Median leaves long-aristate, the midvein strongly raised and prominent throughout, terminating in a conspicuous awn which is half, to equal, the length of the lamina. *S. tarapotensis*.
 - x. Median leaves acute to acuminate or short-aristate, the midvein not or slightly prominulous, the awns (if any) not half the length of the lamina.
 - y. Surface of many or most lateral leaves minutely verrucose or spinulose above, at least near the basiscopic margin; megaspores dull

- orange; lateral leaves often with 1–2 false veins subparallel with the true midvein and $\frac{1}{2}$ – $\frac{3}{4}$ its length. *S. porphyrospora*.
- y. Surface of lateral leaves smooth; megaspores white, pale yellow or beige; lateral leaves sometimes with numerous, diminutive, false veins scattered throughout, but lacking long, conspicuous ones.
- z. Rhizophores confined to the proximal half of the stem; branches often flagelliform. *S. cladorrhizans*.
- z. Rhizophores borne throughout stem, from base nearly to apex; branches never flagelliform (although stem apex flagelliform in *S. flagellata*).
- aa. Median leaves acute to short-acuminate, never aristate; branches simple (not again branched) and of subequal length; stem apex not flagelliform. *S. apoda*.
- aa. Median leaves (most of them) caudate to short-aristate; branches reduced in size toward stem apex, at least the proximal ones again branching; stem apex commonly flagelliform. *S. flagellata*.

Selaginella apoda (L.) Spring, in Martius, Flora Brasiliensis 1(2): 119. 1840 (as "*S. apus*"). *Lycopodium apodum* L., Species Plantarum 1105. 1753. *Diplostachyum apodum* (L.) Pal.-Beauv., Prodrome Aethéogamie 107. 1805. *L. albidulum* Sw., Syn. Fil. 183 & 409. 1806. *S. albidula* (Sw.) Spring, Flora 21: 214. 1838.

Thus far, apparently known from a single location in Guatemala, "in roadside ditch, ca. 6,000 ft, Nebaj, El Quiché" from two different collections: Sharp 4578, Feb. 5, 1945, and Proctor 24946, Jun. 27, 1964; found elsewhere in sun or shade, commonly in marshes or swamps, or on wet, clay banks; Canada; United States; Mexico.

Plants terrestrial, heterophyllous throughout; stems stramineous or pale greenish, prostrate, branches simple (not again branching), of subequal length and commonly widely spaced from base to apex, neither branches nor stem apex flagelliform; rhizophores borne throughout, produced from the lower surface of the stem; lateral leaves 1.5–2.5 mm long, most of them 1.2–1.5 times as long as broad, well spaced, membranaceous, translucent, surfaces glabrous and smooth, with a single midvein, but lacking false veins, the margins minutely serrulate to subentire, and commonly lined with a pale, narrow band of tissue; axillary leaves similar to lateral ones; median leaves 1–1.5 mm long, acute to short-acuminate, margins subentire to minutely serrulate and with a pale, narrow band of tissue; strobili 3–6 mm long, slightly to scarcely tetragonous; sporophylls 1–2 mm long, scarcely to strongly carinate, commonly spreading at maturity; megaspores white to pale yellow; microspores bright to deep orange.

There has been much confusion concerning the nomenclature of this species. It is often found in the literature, and in herbaria, as *S. apus* (L.) Spring, *S. apoda* (L.) Morren, and *S. apoda* (L.) Fern. For complete discussion, see Morton in Amer. Fern J. 57: 104–106. 1967.

In addition to the characters used in the key, *S. apoda* often can be separated from *S. flagellata* (and similar species) by the very broad lateral leaves. Many of these are often nearly as broad as long, whereas most lateral leaves in *S. flagellata*, *S. cladorrhizans*, and *S. porphyrospora* are two to two and a half times as long as broad.

Selaginella cladorrhizans A. Br., Ann. Sci. Nat. Bot. 5(3): 282. 1865.

In forests and wooded ravines, commonly on clay banks, but occasionally found in wet, marshy meadows, 30–2,850 m; Izabal; Petén; Quezaltenango; San Marcos.

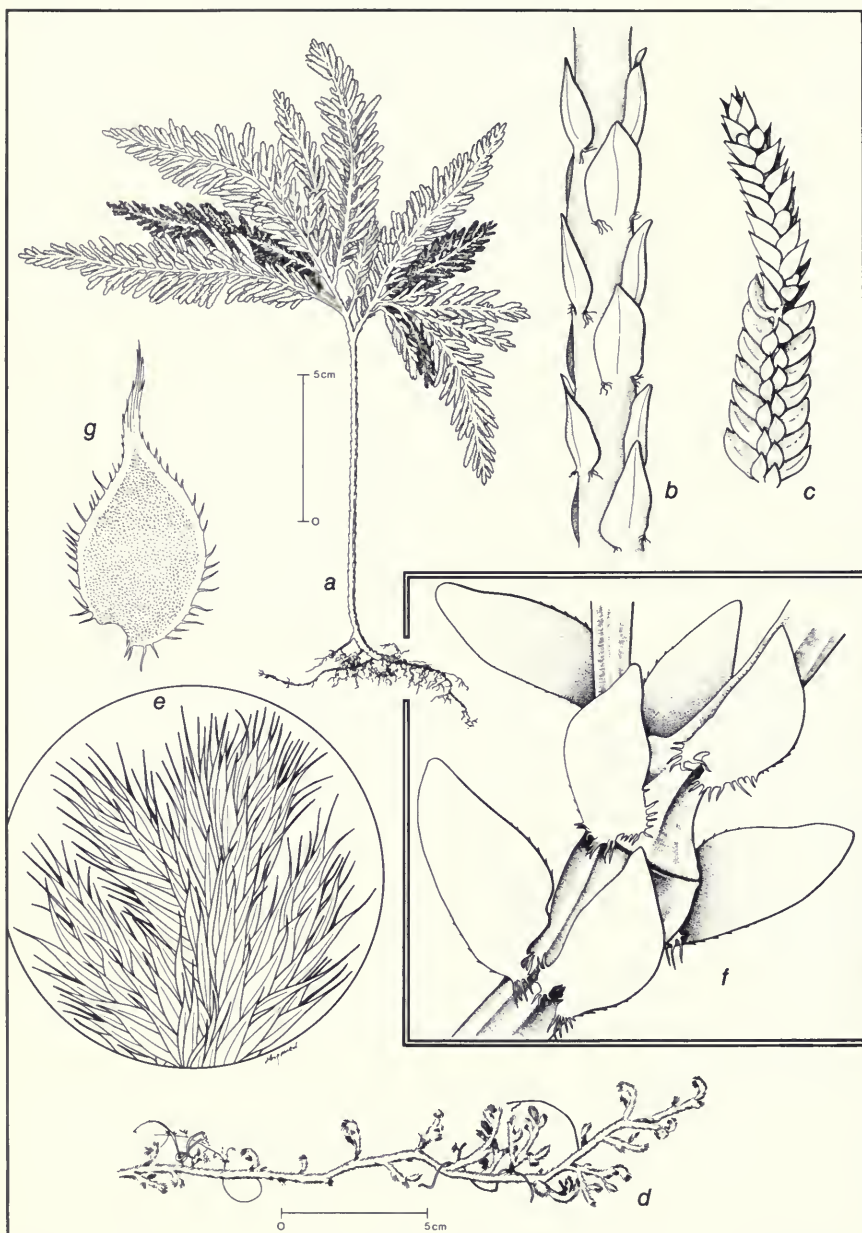


FIG. 9. *Selaginella*. a–c, *S. umbrosa*: a, habit, $\times \frac{1}{2}$; b, portion of stem, $\times 9$; c, tip of branch, with sterile leaves and sporophylls, $\times 9$. d–e, *S. steyermarkii*: d, habit, $\times \frac{1}{2}$; e, tip of branch, $\times 9$. f, *S. galeottii*, part of stem and base of branch, with detail of node, $\times 9$. g, *S. pallescens* var. *pallescens*, median leaf, $\times 25$.

Mexico; British Honduras; Honduras; Costa Rica; Panama; Trinidad and Tobago; Colombia; Venezuela.

Plants terrestrial, heterophyllous throughout; stems stramineous or pale greenish, prostrate to slightly ascending, never caespitose, branching from base to apex, branches sometimes greatly elongated and/or flagelliform; rhizophores borne in the proximal $\frac{1}{2}$ of the plant and produced from the lower surface of the stem; lateral leaves 1.5–2.5 mm long, (1.5–) 2–2.5 times as long as broad, well spaced, sometimes lustrous (but not silvery) beneath, thin-herbaceous to membranaceous and most of them translucent, surfaces glabrous and smooth, with a true midvein and (frequently) several to numerous, very short false veins scattered between midvein and margin, the margins entire to minutely serrulate; axillary leaves similar to lateral ones; median leaves 1–2 mm long, sometimes acuminate, but more commonly caudate to short-aristate, the awn (if any) rarely half the length of the lamina, margins entire to serrulate; strobili 3–8 mm long, subtetragonous; sporophylls 1–1.5 mm long, slightly to moderately carinate, often spreading at maturity; megaspores white or pale yellow (sometimes orange at the proximal pole); microspores bright orange to deep reddish orange.

This and *S. porphyrospora* may be very difficult to separate. See discussion of the latter for further comparison.

Selaginella convoluta (Arn.) Spring, in Martius, Flora Brasiliensis 1(2): 131. 1840. *Lycopodium convolutum* Arn., Mem. Wern. Nat. Hist. Soc. 5: 199. 1824 (reprint in Mém. Soc. Hist. Nat. Paris 1[2]: 347. 1824) (not Desv. 1814). *S. longispicata* Underw. ex Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 287, t. 10. 1896.

In forests or wooded ravines, on rocky slopes, rock outcrops or cliffs, 250–420 m; Chiquimula; Zacapa. Greater Antilles; Mexico (Yucatan); Honduras; Colombia to British Guiana; Brazil; Bolivia; Paraguay. *Much-coc*, or *mutz-coc* (Yucatan); *doradilla* (Yucatan); *conquilla* (fide Steyermark, Zacapa).

Plants terrestrial to epipetric, heterophyllous throughout; stems yellowish green to castaneous, densely caespitose, branched throughout, commonly forming rosettes, tightly curling inward when dry; rhizophores uncommon, produced from the lower surface of the stem; lateral leaves 1.5–3 mm long, strongly imbricate, obliquely elliptic-lanceolate, acute to rostrate, the margins subtire to serrulate, or setulose at base, young leaves silvery beneath, many mature ones castaneous on the acroscopic side, turning wholly dark brown in age; median leaves 1–2.5 mm long, obliquely elliptic-lanceolate, acute to rostrate or short-aristate, the margins serrulate to setulose, green throughout or occasionally with inconspicuous, narrow, pale margins; strobili 6–28 mm long, sharply tetragonous, bearing 2 longitudinal rows each of megasporangia and microsporangia; sporophylls 1–1.5 mm long, sharply carinate; megaspores white, strongly tuberculate; microspores bright orange, shed in tetrads surrounded by a common wall.

Besides the characters used in the key, *S. convoluta* usually can be separated from *S. pallescens* in that most median leaves are similar in shape to the lateral leaves and are nearly the same size. In *S. pallescens*, the median leaves are quite obviously smaller, and relatively broader, throughout than the lateral ones.

Selaginella lepidophylla (Hook. & Grev.) Spring of Mexico and southwestern United States has the stems densely caespitose and in a rosette just as *S. convoluta*, but the old leaves turn red, not castaneous, and the median leaves are obtuse to hardly acute and have broad, conspicuous white or translucent margins.

The colloquial name "conquilla," used in Zacapa, apparently refers to the sharply carinate sporophylls which form the strongly tetragonous strobili. In Yucatan, the species has been used as a native remedy for respiratory ailments, and as a sedative. An infusion is made by soaking the whole plant in water, sweetening, and taking as a cold drink.

Selaginella delicatissima A. Br., Index Sem. Hort. Bot. Berol. App: 13. 1857 (not Linden 1856, *nom. nud.*). *S. saccharata* A. Br., Ann. Sci. Nat. Bot. V, 3: 272. 1865. *S. sanguinolenta* Liebm. ex Fourn., Mex. Pl. 148. 1872.

Apparently known from Guatemala by a single collection: under bushes, Santa Rosa, Baja Verapaz, 1,600 m, Tuerckheim II-2180; and from Honduras by a single collection: on river rocks in pine forest, 900 m, Ocotepeque, *Molina* 22371; otherwise confined to Mexico: on soil or occasionally on rocks, on banks of streams, rivers or ravines, 600–2,200 m.

Plants terrestrial, occasionally epipetric, heterophyllous; stems prostrate, solitary or remote, never caespitose, stramineous, or light yellowish brown at base, branched nearly from the base; rhizophores commonly borne throughout, produced from the lower surface of the stem; lateral leaves 1.2–2.2 mm long, well spaced on main stem, approximate to contiguous on the branches, older ones often pinkish or reddish brown, ovate to elliptic, acute or subacute, cordate or subcordate at base, margins subentire, but ciliate toward the base; axillary leaves oblong to elliptic or elliptic-lanceolate, acute or subacute, subcordate to deeply cordate at base, ciliate in the proximal portion; median leaves 1–2.5 mm long, narrow-ovate, acute or (rarely) short-acuminate, irregularly cordate at base, at least those of stem and main branches with 1 free, rather conspicuous lobe or auricle, the margins setose to ciliate, and commonly long-ciliate at base; strobili 5–18 mm long, rather strongly tetragonous; sporophylls 1–1.8 mm long, rather sharply carinate; megaspores yellow to orange-yellow; microspores deep orange.

Selaginella eurynota A. Br., Ann. Sci. Nat. Bot. V, 3: 293. 1865.

Prostrate or decumbent, on floor of wet forests or thickets, or on moist, shaded banks, 200–1,800 m; Escuintla; Quezaltenango; Retalhuleu; San Marcos; Suchitpequez. Southern Mexico (Chiapas); Nicaragua; Costa Rica; Panama.

Plants terrestrial, heterophyllous throughout; stems prostrate or decumbent, branched throughout, articulate; rhizophores springing from the upper surface of the stem for $\frac{1}{3}$ – $\frac{3}{4}$ of its length; lateral leaves commonly spreading from the axes at 90° angles, 3–6 mm long, narrowly oblong to elliptic-lanceolate, acute or subacute, the margins entire to serrulate (sometimes ciliate toward base and then the cilia 0.1–0.2 mm long), slightly to deeply cordate at base, the basal acroscopic lobe commonly broadly arching over and directed down along the axis; axillary leaves linear- to elliptic-oblong, the margins subentire to serrulate, the base slightly to deeply cordate with the lobes subparallel, contiguous (rarely imbricate) and usually abundantly ciliate (cilia 0.1–0.2 mm long); median leaves 1.5–2.5 mm long, obliquely ovate-acuminate, the margins entire to serrulate, peltate, i.e., a single rounded to subacute lobelike projection extending below the point of attachment, this ca. $\frac{1}{3}$ – $\frac{1}{4}$ the length of the leaf; strobili 5–13 mm long, slightly to strongly tetragonous, bearing a single megasporangium at base; sporophylls 1–2 mm long, acute or acuminate, slightly to sharply carinate; megaspores yellowish or beige, with strongly pronounced, white, reticulate ridges; microspores tawny.

This is closely related to *S. horizontalis* (Presl) Spring of southern Central America and perhaps should be considered only a variety of it. The latter has the basal lobes of axillary leaves mostly imbricate and bearing cilia 0.3 to 0.5 mm long. Axillary leaves of *S. eurynota* have their lobes contiguous (only rarely imbricate) and with cilia 0.2 mm long or less. Besides these, there appear to be few, if any, other differences in the two taxa.

Selaginella flagellata Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 228. 1843.

In forests and wooded ravines, on wet banks or on rocks, 30–900 m; Alta Verapaz; Izabal; Petén; Retalhuleu; Santa Rosa. Mexico; Nicaragua; Costa Rica; Panama; Trinidad and Tobago; Colombia to the Guianas, south to Brazil and Bolivia.

Plants terrestrial or epipetric, heterophyllous throughout; stems stramineous to pale greenish, prostrate, branching from base nearly to apex, at least the proximal branches again once- or twice-branched, gradually reduced in size toward the stem apex, the apex commonly flagelliform; rhizophores borne throughout, produced from the lower surface of the stem; lateral leaves 1.5–3 mm long, 1.5–2 times as long as broad, contiguous to well spaced, sometimes lustrous beneath, but not silvery, thin-herbaceous to membranaceous and commonly translucent, surfaces glabrous and smooth, with a true midvein and often with several to many very short false veins scattered between midvein and margin, the margins entire to serrulate; axillary leaves similar to lateral ones, but often relatively narrower; median leaves 1–1.5 mm long, sometimes acuminate, but more commonly caudate to short-aristate, the awn (if any) rarely half the length of the lamina, margins entire to serrulate and often with a very narrow band of whitish tissue; strobili 3–8 mm long, subtetragonous; sporophylls 1–1.5 mm long, carinate, often spreading at maturity; megaspores white, microspores light orange.

This may be nothing more than a variant of *S. cladorrhizans*, from which it differs only in a few ways. In *S. flagellata*, the stems are consistently flagelliform and bear rhizophores nearly or quite to the apex. Stems of *S. cladorrhizans* bear rhizophores only near the base or, at most, only along the proximal half and are not flagelliform (although some of the branches may be greatly elongated and/or flagelliform). Color of the spores differs somewhat, but not sharply or consistently: megaspores of *S. flagellata* are always white, and microspores, commonly a light orange; megaspores of *S. cladorrhizans* may be white, but in many specimens, are pale yellow, and microspores vary from bright to deep orange.

***Selaginella galeottii* Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 230. 1843.**

Erect to suberect, in wet forests and thickets or on shaded banks, occasionally in clearings and pastures, 300–1,800 m; Alta Verapaz; Baja Verapaz; Huehuetenango; Izabal; San Marcos. Mexico; British Honduras; Honduras; El Salvador; Nicaragua; Costa Rica. *Oxikak* (*fide* Standley, Alta Verapaz).

Plants terrestrial, very rarely epipetric, heterophyllous throughout; stems erect to suberect, articulate, branched throughout, or sometimes with few or no branches in the proximal half of the main stem; rhizophores present at base of stem or along $\frac{1}{2}$ its length, produced from the upper surface of the stem; lateral leaves 2.5–5 mm long, obliquely oblong to elliptic-lanceolate or ovate, acute, the margins entire to serrulate, ciliate at the rounded to subcordate base (if subcordate, then acroscopically with a small, narrow lobe, basiscopically geniculate); axillary leaves elliptic or lanceolate, most of them ciliate at base, auricles lacking or, rarely, minute and inconspicuous; median leaves 1.5–3 mm long, oblique-lanceolate or -ovate, acute or sometimes short-acuminate, the margins entire to serrulate, ciliate at the biauriculate base, the auricles subequal to unequal, at least one of them large and conspicuous; strobili 4–18 mm long, strongly to slightly tetragonous, bearing a single, megasporangium at base; sporophylls 1–1.5 mm long, acute to acuminate, slightly to sharply carinate; megaspores gray, beige, or tawny, with pronounced, white reticulate ridges; microspores beige, tawny, or pale yellow.

This has been confused in herbaria with *S. stellata* Spring (= *S. conduplicata* Spring) of South America, to which it is closely related. Axillary leaves of the latter are conspicuously biauriculate, with each auricle long, narrow, and spurlike, and lateral and axillary leaves are eciliate. Axillary leaves of *S. galeottii* are rarely auriculate or auricles, when present, are minute and inconspicuous; moreover, most lateral and axillary leaves have at least a few long cilia toward the base or at their point of attachment.

***Selaginella guatemalensis* Baker, J. Bot. 21: 243. 1883 (pro parte). *S. lehmannii* Hieron., Hedwigia 43: 33. 1904 (type from near Puxala, Baja Verapaz, Lehmann**

1329). *S. pansamalensis* Hieron., *tom. cit.* 35 (type from Pansamalá, Alta Verapaz, Tuerckheim 653).

In forests and wooded ravines, on rocky hillsides or stream banks, or on limestone cliffs, 300–1,800 m; Alta Verapaz (type from Cobán, *Salvin & Godman s.n.*); Baja Verapaz; Huehuetenango; San Marcos. Southern Mexico; Honduras.

Plants terrestrial or epipetric, heterophyllous throughout; stems stramineous, prostrate or ascending, approximate to remote, never caespitose, branching throughout; rhizophores mostly stout and straight, larger ones 0.4–0.9 mm thick, 4–18 cm long, borne from base of stem nearly to apex, produced from the lower surface of the stem; lateral leaves (larger ones) 2–4 mm long, well spaced on the main stem, approximate to contiguous or slightly imbricate on the branches, spreading from the axes at 30°–60° angles, often silvery beneath, obliquely lanceolate or oblong-lanceolate, obtuse or subacute, inequilateral at base, broadly rounded acroscopically, narrowly rounded to subtruncate basiscopically, margins entire to serrulate, setose to ciliate toward the base, occasionally with 1–2 long cilia at very base; axillary leaves like the lateral ones, but consistently lanceolate and subacute, equilateral and broadly rounded at base; median leaves 1–2.2 mm long, ovate to elliptic, obviously longer than broad, acuminate, margins long-setose or occasionally ciliate, green throughout or with an inconspicuous pale or whitish band of tissue 1 cell wide, obliquely subcordate at base, approximate on the main stem, approximate to slightly imbricate on the branches; strobili 4–20 mm long, strongly to weakly tetragonous; sporophylls 1–1.5 (–2) mm long, carinate, usually spreading at maturity; megaspores white; or off-white; microspores pale orange.

Selaginella hoffmannii Hieron., *Hedwigia* 41: 184. 1902.

In forests, along stream banks or on banks of wooded ravines, occasionally on rocks or on exposed clay banks, 30–1,800 m; Alta Verapaz; Escuintla; Huehuetenango; Jutiapa; Quezaltenango; Retalhuleu; Santa Rosa; Sololá. Mexico to Panama.

Plants terrestrial, occasionally epipetric, erect, heterophyllous, but homophyllous toward base of stem; stems solitary or remote, commonly roseate or pinkish at or near the base, never caespitose, unbranched in the proximal $\frac{1}{2}$ – $\frac{1}{4}$ (or sometimes with branches almost to the base); rhizophores few, mostly basal, produced from the lower surface of the stem; lateral leaves 1–3 mm long, well spaced on main stem, becoming contiguous or slightly imbricate on the branches, obliquely oblong- or elliptic-lanceolate, acute or subacute, margins subentire to serrulate (rarely ciliate near base), often becoming roseate or pinkish toward base of stem; axillary leaves elliptic-lanceolate, acute or subacute, subentire to serrulate, becoming ciliate or ciliate at base; median leaves 0.8–2 mm long, obliquely curving back across the axis and the opposing leaf, ovate, aristate, irregularly cordate or subcordate at base, here often with an adnate, lobelike projection on one side, the margins with a narrow but conspicuous pale green to whitish band of tissue, remotely serrulate or setose or sometimes with a few cilia at base; strobili to 1 cm long, somewhat to strongly tetragonous; sporophylls ca. 1 mm long, sharply carinate; megaspores pale yellow, beige or whitish; microspores bright orange.

Selaginella hoffmannii belongs to that complex of specimens having their stems erect, inarticulate, and unbranched and homophyllous in the proximal portion (although in this species the stems are homophyllous only at or near the base). It is similar to *S. umbrosa* in the reddish coloration, but in the latter, the stems are rather deep red nearly throughout, whereas in *S. hoffmannii*, the color is a pale roseate or pinkish hue and frequently is confined to (or near) the very base. Furthermore, the color sometimes fades almost completely in dried specimens. Most median leaves, as well as a few lateral ones, have a very narrow, pale or whitish band of tissue along the margin, which is quite apparent even with low magnification. However, leaves of other Guatemalan species in the complex are

wholly green, or a few may have a very inconspicuous pale band, and this is scarcely discernible, even at higher magnification.

Selaginella huehuetenangensis Hieron., Hedwigia 43: 32. 1904.

In forests, thickets and clearings, on forest floor, rocky banks, or occasionally on rocky ledges of cliffs, 100–1,500 m; Alta Verapaz; Huehuetenango (type from between Santa Cruz Almar and Ixcán, *Bernoulli & Cario* 178); Izabal; Petén; Quezaltenango; San Marcos. British Honduras; Honduras; Nicaragua; Costa Rica; Panama.

Plants terrestrial, rarely epipetric, heterophyllous throughout, often crowding together and forming mats with other plants; stems stramineous, prostrate, remote, never caespitose, branching throughout; rhizophores mostly stout and straight, larger ones 0.3–0.7 mm thick, 4–12 cm long, borne from base of stem to apex, produced from the lower surface of the stem; lateral leaves 1–2 mm long, well spaced on the main stem, well spaced to contiguous (rarely slightly imbricate) on the branches, most of them spreading from the axes at 45°–60° angles, often silvery beneath, narrow-ovate to obliquely lanceolate or elliptic-lanceolate, acute or subacute, broadly rounded to subcordate at base acroscopically, abruptly rounded or subtruncate basiscopically, margins entire to serrulate, often with a whitish narrow band of tissue, long-ciliate in the proximal portion, the length of some cilia equalling $\frac{1}{4}$ – $\frac{1}{2}$ the breadth of the leaf; axillary leaves like the lateral leaves, but consistently lanceolate and subacute, equilateral and broadly rounded at base; median leaves 1–1.5 mm long (including the 0.3–0.6 mm awn), ovate to elliptic, leafy portion obviously longer than broad, conspicuously aristate, margins long-setose to ciliate, with a broad to narrow whitish band of tissue 1 to several cells wide (rarely green throughout), obliquely subcordate at base, well spaced on the main stem, contiguous to somewhat imbricate on branches; strobili 4–8 mm long, subtetragonous; sporophylls 1–1.8 mm long, carinate, appressed to somewhat spreading at maturity; megaspores white; microspores pale to bright orange.

This may be confused with both *S. guatemalensis* and *S. idiospora*, but all three may be distinguished by the characters used in the key. *Selaginella chiapensis* A. R. Smith from adjacent Chiapas, Mexico, is yet another species in this complex. Indeed, *S. chiapensis* seems to be intermediate between *S. huehuetenangensis* and *S. idiospora*, for it has most of the lateral leaves spreading at ca. 90° from the axes as in *S. idiospora*, and it has the lateral leaves silvery beneath as is often the case in *S. huehuetenangensis*. However, in *S. chiapensis*, the median leaves are acuminate, whereas, in both *S. huehuetenangensis* and *S. guatemalensis*, they are conspicuously aristate.

Selaginella idiospora Alston, Bull. Brit. Mus. (Nat. Hist.), Bot. 1: 246. 1955.

In forests, in soil or on rocks, often along banks of streams and rivers, 30–920 m, Alta Verapaz (type from vicinity of Secanquim, altitude 550 m, *Pittier* 191); Izabal. Honduras.

Plants terrestrial or epipetric, heterophyllous throughout; stems prostrate, remote, never caespitose, stramineous, branching throughout; rhizophores mostly stout and straight, larger ones 0.3–0.6 mm thick, 5–15 cm long, borne from base of stem to apex, produced from the lower surface of the stem; lateral leaves 1.5–3 mm long, crowded throughout, most of them spreading from the axes at a 90° angle, oblong-lanceolate, slightly falcate, acute or subacute, broadly rounded at base acroscopically, abruptly rounded to truncate basiscopically, margins subentire, ciliate toward base, at least acroscopically; axillary leaves similar to lateral ones, but relatively shorter and narrower; median leaves slightly imbricate, 1–2 mm long (including awn), leafy portion nearly as broad as long, most of them (especially those on main stem) nearly circular, conspicuously aristate, margins long-setose

to ciliate, green throughout, obliquely cuneate to obtuse at base; strobili 4–10 mm long, tetragonous; sporophylls 1–1.5 mm long, sharply carinate, tightly appressed, or somewhat spreading at maturity; megaspores white to pale beige; microspores dull orange.

A new species, *S. chiapensis* A. R. Smith, from Chiapas, Mexico (Amer. Fern J. 70: 25. 1980), has been described as being closely related to *S. idiospora*. For further comparisons see discussion under *S. huehuetenangensis*.

Selaginella illecebrosa Alston, Bull. Brit. Mus. (Nat. Hist.), Bot. 1: 239. 1955.

In forests, along streams and river banks, often among rocks, 50–150 m; Izabal (type from along stream tributary to Río Frío, *Steyermark* 41579); southern Mexico; Honduras.

Plants commonly terrestrial, erect, heterophyllous, but homophyllous as to the stem below the leafy portion; stems solitary or remote, never caespitose, unbranched in the proximal $\frac{1}{3}$ – $\frac{2}{3}$, stramineous; rhizophores few, basal, produced from the lower surface of the stem; lateral leaves 2–5 mm long, approximate to well spaced or, on the branches, often slightly imbricate, oblong- to elliptic-lanceolate, acute, margins entire to serrulate, but conspicuously ciliate at base, and there usually rounded basiscopically, broadly auriculate acroscopically; axillary leaves elliptic- or oblong-lanceolate, acute or subacute, cordate to biauriculate at base, the margins subentire, but ciliate at base; median leaves 1–4 mm long, oblique-ovate, short-aristate, subcordate to biauriculate at base, the margins essentially entire, but often with 2 or 3 cilia at very base; strobili 3–9 mm long, rather sharply tetragonous; sporophylls to 1 mm long, sharply carinate; megaspores white, beige, or cream-colored; microspores orange.

This and *S. oaxacana* can be further separated by the character of the axillary leaves. In the latter, the base of these leaves is not or scarcely cordate, with cilia only a few and short or lacking. Axillary leaves in *S. illecebrosa* are conspicuously ciliate at the cordate or biauriculate base.

Selaginella martensii Spring, Monographie des Lycopodiacees 2: 129. 1850 (preprint of Mém. Acad. Roy. Sci. Belgique 24. 1850). *S. solmsii* Bak., Handbook of the Fern Allies: 56. 1887 (type from Palohueco, Costa Grande [Huehuetenango?], *Bernoulli & Cario* 181). *S. estrellensis* Hieron., Hedwigia 41: 200. 1902.

In forests and thickets, usually on shaded slopes and ravine banks, 650–2,000 m; Alta Verapaz; Baja Verapaz; Quezaltenango; El Quiché; Retalhuleu; San Marcos; Suchitepéquez. Mexico to Panama.

Plants terrestrial, heterophyllous; stems erect to decumbent, solitary or remote, never caespitose, stramineous or yellow-green, branched nearly from the base; rhizophores borne in the proximal $\frac{1}{2}$ of the plant (but occasionally occurring much nearer the apex), produced from the lower surface of the stem; lateral leaves (2–) 3–6 mm long, approximate to well spaced on the main stem, contiguous to slightly imbricate on the branches, dull to moderately lustrous above, scarcely to highly lustrous beneath, mostly oblong, to lanceolate, obtuse to somewhat acute, inequilaterally rounded at base, more strongly produced acroscopically and here often conspicuously overlapping the axis, the margins entire to setose, often conspicuously ciliate at or toward the base; axillary leaves oblong to lanceolate or deltoid-lanceolate, obtuse to somewhat acute, rounded to truncate at base, the margins entire to setulose, or often ciliate at or toward the base; median leaves 1.5–3.5 mm long, elliptic, long-aristate, the awn $\frac{1}{2}$ as long as or equalling the rest of the leaf, irregularly cordate at base, with at least 1 free, conspicuous lobe or auricle, the margins serrulate to setose or ciliate, lobes or auricles nearly always with at least a few cilia; strobili 4–14 mm long, tetragonous; sporophylls acute, to 2 mm long, somewhat to sharply carinate; megaspores white; microspores orange.

This is a species with some highly variable characteristics, the extreme variants of which might be considered distinct varieties or species. The type of *S. estrellensis* (as well as some other specimens examined from Costa Rica) was differentiated from *S. martensii* by Hieronymus and Alston on a series of quantitative characters: lateral leaves *more* acute and *more* cordate, median leaves *more* polished, stems *usually* prostrate and rhizophores *usually* at right angles from the axis. During the course of study on this Flora, most specimens cited by Alston (1955) as *S. martensii* and *S. estrellensis* were carefully compared in all their features, especially the following: leaves lustrous vs. dull, lateral leaves acute vs. obtuse, acroscopic base of lateral leaves slightly vs. strongly and broadly rounded, margin of lateral and/or median leaves subentire vs. ciliate, awns of median leaves equal to vs. half the length of the leaf proper, relative position of rhizophores on the main axis. Not one character remained constantly in opposition with any other. Moreover, each character may be observed on at least a few specimens, anywhere from Mexico to Costa Rica. However, in spite of such variation, all these specimens can be gathered together with at least these features in common among the nonarticulate species: median leaves conspicuously aristate and with at least one free, conspicuous basal lobe or auricle, and most of these ciliate; most lateral leaves oblong and the larger ones 4 to 5 mm long; stems solitary to remote, never caespitose, heterophyllous and branching throughout.

Selaginella mollis A. Br., Ann. Sci. Nat. Bot. V. 3: 276. 1865 (not Fée, 1866).

Not in Guatemala, but to be expected, since it has been found in adjacent Chiapas, Mexico, and in British Honduras; rain forests, wooded ravines and slopes, on rocks or on clay banks; 30–750 m; southern Mexico; British Honduras; Nicaragua to Colombia.

Plants terrestrial or epipetric, heterophyllous; stems prostrate, remote, never caespitose, stramineous or pale green, branching throughout, the branches approximate and pinnately branched, stem and branches often with flagelliform apices; rhizophores filiform, often tortuous, 0.1–0.2 (–0.3) mm thick, rarely more than 2 cm long, borne from base of stem to apex, or sometimes confined to the proximal $\frac{1}{3}$, produced from the lower surface of the stem; lateral leaves 1.2–2.2 mm long, 0.4–1 mm broad, well spaced on the main stem, approximate to contiguous on the branches, narrowly oblong-deltoid, or deltoid on the main stem, acute to subacute, margins entire distally, but conspicuously setose or ciliate at or toward the base, green throughout, without pale or white margins; axillary leaves similar to the lateral leaves, but commonly lanceolate or elliptic-lanceolate; median leaves 0.7–1.5 mm long, obliquely ovate or elliptic, acute to short-aristate, margins serrulate, but setose to ciliate at or near base (at least on one side), obliquely cuneate or subcordate at base, green throughout, without white margins, those of the main stem well spaced, those of ultimate branches contiguous or slightly imbricate; strobili (3–) 4–10 mm long, scarcely to moderately tetragonous; sporophylls 1–1.5 mm long, carinate; megasporophylls white to cream-colored; microspores bright orange.

The habit of this species is highly variable, sometimes with main stem and branches greatly elongated and flagelliform, with rhizophores borne throughout, even to tips of branches and stem; or equally as often, the plants may be broadly ovate, with rhizophores confined to the proximal portion. Also, median leaves may be conspicuously ciliate in their proximal half, along both margins, or they may at first appear to be without cilia. In the latter case, cilia may be lacking from the basiscopic margin, making those setae or cilia on the acroscopic side difficult to discern, since this margin usually lies exactly along the axis, and the processes are transparent or the same color as the axis.

Selaginella oaxacana Spring, *Mongraphie des Lycopodiaceés* 2: 177. 1850 (pre-print of *Mém. Acad. Roy. Sci. Belgique* 24: 1850). *S. wendlandii* Hieron., in Engl. & Prantl, *Die Natürlichen Pflanzenfamilien* 1(4): 683. 1901. *S. costaricensis* Hieron., *tom. cit.* 188 & 683.

In forests, thickets and wooded ravines, along stream and river banks, sometimes in rocky ground or in soil among rock crevices, 300–1,400 m; Alta Verapaz; Baja Verapaz; Huehuetenango; Zacapa. Southern Mexico (type from Chinantla, Oaxaca, *Galeotti 6608 bis*); Honduras; Costa Rica; Panama; Colombia; Ecuador.

Plants commonly terrestrial, erect, heterophyllous, but homophyllous as to the stem below the leafy portion; stems unbranched in the proximal half, stramineous to pale green; rhizophores few, basal, produced from the lower surface of the stem; lateral leaves 2–5.5 mm long, well spaced to contiguous or (rarely) slightly imbricate, oblong- to elliptic-lanceolate, acute or subacute, margins subentire, essentially naked, the base rounded acroscopically, commonly truncate to geniculate basiscopically; axillary leaves elliptic- or oblong-lanceolate, acute or subacute, only slightly or not at all cordate at base, the margins subentire, naked at base or with a very few, short cilia; median leaves 2–6 mm long, ovate or broadly lanceolate, acuminate to short-aristate, cordate to subcordate or unequally auricled at base, the margins entire to remotely serrulate, or sparsely setose or ciliate at base; strobili to 1.5 mm long, rather sharply tetragonous; sporophylls to 1 mm long, sharply carinate; megaspores white to cream-colored; microspores beige or tawny to very pale orange.

This is closely related to *S. illecebrosa*, under which see further comparison.

Selaginella ovifolia Baker, *J. Bot.* 22: 90. 1884.

Not in Guatemala, but to be expected there; found in shaded ravines, banks and hillsides, 30–700 m; British Honduras; Jamaica; Haiti; Puerto Rico.

Plants terrestrial, heterophyllous; stems prostrate, remote, never caespitose, although often forming tangled masses with others, stramineous or pale green, branching from base to apex, the branches remote, often simple, or with a few, short branchlets; rhizophores filiform and tortuous, less than 0.1 mm thick, rarely more than 2 cm long, borne from base of stem to apex, produced from the lower surface of the stem; lateral leaves 0.6–1.5 mm long, 0.5–1 mm broad, well spaced on the main stem, slightly imbricate on the branches, ovate to broadly elliptic or nearly circular, acute or subacute, margins setose to ciliate, broad-cuneate to obtuse or broadly rounded at base, green throughout, or rarely with a faint, narrow, pale margin; axillary leaves like the lateral leaves, but usually somewhat narrower; median leaves 0.4–0.8 mm long, ovate to lanceolate, acuminate to short-aristate, margins setose to ciliate, irregularly subcordate and obliquely attached at base, green throughout, or rarely with a faint, narrow, pale margin, those of the main stem well spaced, those of the ultimate branches contiguous or slightly imbricate; strobili 1–2 mm long, often consisting of only 1–2 sets of sporophylls; sporophylls 0.6–1 mm long, slightly to strongly carinate, widely spreading at maturity; megaspores white or cream-colored; microspores deep or bright orange.

Selaginella pallescens (Presl) Spring, in Martius, *Flora Brasiliensis* 1(2): 132. 1840.

Plants epipetric or terrestrial, heterophyllous, but homophyllous as to the main stem below the leafy portion; stems densely caespitose and often forming rosettes or, if not caespitose, then (occasionally) approximate to crowded, branching from the base or only in the distal half; rhizophores few, mostly basal, produced from the lower surface of the stem; lateral leaves 1–3 mm long, approximate, contiguous, or slightly imbricate, obliquely elliptic-lanceolate to broad-ovate, acute to acuminate or short-aristate, margins serrulate to (near the base) ciliate, young leaves silvery beneath or occasionally dull green, older leaves light brown to tawny or whitish or (sometimes in var. *acutifolia*) streaked or tinged with

pink; median leaves 0.6–2 mm long, ovate or elliptic-lanceolate, acute to acuminate or aristate, green throughout above or (commonly) with conspicuous pale or white margins, these serrulate, setose or ciliate; strobili 2–12 mm long, scarcely to sharply tetragonous; sporophylls 1.5–2 mm long, slightly to sharply carinate; megaspores white or gray-white to beige or very pale yellow, smooth-surfaced to low-papillose or -tuberculate; microspores bright orange or reddish orange.

This is a highly variable species, growing in the soil or on rocks, in shade or in exposed locations, from sea level to over 3,000 m. It occurs in Mexico, Central America, Cuba, Jamaica, and in part of South America. Like *S. convoluta*, it is primarily a caespitose plant, but sometimes the stems are slightly spaced. The typical and one other variety are recognized in Guatemala, but a thorough study of the species throughout its range may delineate some other varieties, or may reveal that other species should be included with it.

***Selaginella pallescens* var. *acutifolia* Stolze, Amer. Fern J. 71: 51. 1981.**

In forests or wooded ravines, commonly on rocks, cliffs or rock outcrops, 200–550 m; Chiquimula; Escuintla; Jutiapa; Zacapa (type from rocky hills, 2 miles south of Zacapa, *Steyermark* 29293); Honduras; El Salvador; Nicaragua; Costa Rica.

Plants epipetric, rarely terrestrial (in Guatemala); stems reddish, at least at base; lateral leaves acute, rarely subacute, sometimes a few of the older ones becoming streaked or tinged with pale red; median leaves acute at apex, or a few of them merely subacute.

This variety prefers low altitudes and, at least in Guatemala, rocky habitats. The typical variety is found occasionally near sea level, but most commonly occurs between 800 and 2,500 m. It, too, is found in rocky situations, but seems to be equally at home on the forest floor.

***Selaginella pallescens* var. *pallescens*. *Lycopodium pallescens* Presl, Rel. Haenk. 1: 79. 1825. *L. cuspidatum* Link, Hort. Reg. Bot. Berol. 2: 161. 1833. *S. cuspidata* (Link) Link, Fil. Spec. 158. 1841. *S. cuspidata* var. *elongata* Spring, Monographie des Lycopodiacees 2: 67. 1850 (preprint of Mém. Acad. Roy. Sci. Belgique 24. 1850). *S. microdendron* Bak., J. Bot. 23: 116. 1885. *S. harrisii* Underw. & Hieron., in Urban, Symb. Antill. 7: 162. 1912. *S. millspaughii* Hieron., Hedwigia 58: 285. 1917.**

In forests, thickets, shaded ravines, in pastures or on open banks, on rocks or rocky soil or on forest floor, (100–) 400–3,100 m; thus far reported from all departments except Izabal and Totonicapán; Cuba; Jamaica; Mexico to Colombia and Venezuela; Brazil.

Plants terrestrial or epipetric; stems stramineous or pale green; lateral leaves acuminate to aristate at apex, older ones tawny to dull whitish; median leaves acuminate to aristate.

Alston (1955) and more recent authors have maintained *S. microdendron* as a distinct species, based on the acuminate (not aristate) lateral leaves, the newer leaves dull green (not silvery) beneath, the old leaves reddish brown (not tawny), the stems branching above (not below) the middle, and the lowest branch longer (not shorter) than those above it. After studying several hundred specimens in the *S. pallescens* complex, I find that none of these characters is consistent. For example, there are plants in which the lowest branch is nearly as long as the rest of the main stem, but springs from the proximal third to fourth of the stem (not the upper half). Then, when the branching pattern is consistent, by Alston's formula, the color and shape of the lateral leaves are not consistent with this. Furthermore,

even in the type of *S. microdendron*, the lateral leaves are not "dull green," but lustrous. Very rarely, in the entire *S. pallescens-microdendron* complex, are leaves ever truly "dull" beneath.

So freely intermixed are the supposed diagnostic characters that I cannot recognize *S. microdendron* at even the infraspecific level. This is a good example of one of those highly variable species which takes on somewhat different aspects according to the extremes of habitat in which it occurs. (Those plants which have been considered to be *S. microdendron* usually grow in soil on the forest floor, whereas the densely caespitose plants branching from the base commonly grow on or among rocks.)

Here also must probably be included *S. pulcherrima* Liebm. ex Fourn. of Mexico. I have not seen the type, but from the description and Alston's remarks, it must be the same.

Selaginella porphyrospora A. Br., Ann. Sci. Nat. Bot. 5(3): 286. 1865. *S. binervis* Liebm. ex Baker, J. Bot. 22: 112. 1884 (not Liebm. ex Fourn. 1872, *nom. nud.*). *S. bernoullii* Hieron., Hedwigia 41: 192. 1902 (type from El Quiché, "inter Cubulco et Joyabaj," 1870, *Bernoulli* 1121).

In forests or wooded ravines, on clay banks, logs or rocks, often along stream banks or near waterfalls, 900–2,800 m; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; San Marcos; Sololá; Suchitepéquez; Totonicapán; Zacapa. Mexico to Panama; Colombia.

Plants terrestrial or epipetric, heterophyllous throughout; stems stramineous or pale greenish, prostrate to ascending, never caespitose, branching from base to apex, branches sometimes greatly elongated and/or flagelliform; rhizophores borne in the proximal half of the plant (or very rarely throughout) and produced from lower surface of stem; lateral leaves 1.2–2.8 mm long, (1.5–) 2–2.5 times as long as broad, well spaced, sometimes lustrous (but not silvery) beneath, opaque and firm-herbaceous to (very rarely) membranaceous, the surface of many or most of them minutely verrucose or spinulose above, at least near the basiscopic margin, frequently with 1–2 false nerves subparallel with the true midvein and $\frac{1}{2}$ – $\frac{3}{4}$ its length, acute, margins entire or subentire; axillary leaves similar to lateral ones; median leaves 1–2 mm long, sometimes acuminate, but more commonly caudate to short-aristate, the awn (if any) rarely half the length of the lamina, margins entire to serrulate; strobili 4–12 mm long, tetraginous; sporophylls 1–1.5 mm long, carinate, often spreading at maturity; megaspores dull orange; microspores bright orange to deep reddish orange.

With this perhaps should be included *S. moritziana* Spring of Colombia and Venezuela. Fournier (Mexicanas Plantas, 1872) listed *S. binervis* as a synonym of *S. moritziana*, but I have not seen the type of the latter, and hesitate to make a firm judgment.

Selaginella porphyrospora is poorly named, for none of the spores are purple. Megaspores at their darkest are merely dull orange, while microspores range from bright orange to a deep reddish orange. This species and *S. cladorrhizans* are so similar that only very close observation, under high (ca. 15×) magnification, will separate them. The verrucose or spinulose lateral leaves (toward the basiscopic margin) is the strongest character, but not all the leaves exhibit this feature. The one or two long, false veins is another good character, but some specimens can be found with these totally absent or so obscure as to be virtually unnoticed. There are a handful of Guatemalan specimens with rather deep orange megaspores, but

lacking spinulose or "bi-nerved" lateral leaves. These specimens cannot be placed with any degree of certainty.

Selaginella reflexa Underw., Bull. Torrey Bot. Club 21: 268. 1894. *S. carioi* Hieron., in Engl. & Prantl, Die Natürlichen Pflanzenfamilien 1(4): 688. 1901 (type from Río Motagua, between Barbasco and Gualan, Zacapa, Bernoulli 955).

In forests, on rocks or limestone cliffs, occasionally on clay banks, 150–500 m; Alta Verapaz; Baja Verapaz; El Progreso; Zacapa. Mexico.

Plants commonly epipetric, occasionally terrestrial, heterophyllous; stems prostrate, remote, never caespitose, although often forming tangled masses with others, stramineous, branching throughout; rhizophores filiform, often tortuous, 0.05–0.1 mm thick, rarely more than 2 cm long, borne from base of stem to apex, produced from the lower surface of the stem; lateral leaves 0.8–1.6 mm long, well spaced on the main stem, approximate to slightly imbricate and strongly ascending on the branches, oblong to nearly circular, obtuse to subacute, margins denticulate to ciliolate and with a conspicuous band of white tissue throughout, rounded at base; axillary leaves similar to lateral ones; median leaves 0.5–1.5 mm long, ovate to lanceolate, acuminate to short-aristate, margins setose to ciliate and with a conspicuous band of white tissue throughout, irregularly cordate at base, those of the ultimate and penultimate branches strongly imbricate; strobili 2–5 mm long, somewhat tetragonous; sporophylls 0.8–1.5 mm long, somewhat carinate, widely spreading at maturity; megaspores white to pale or orange-yellow; microspores bright orange.

Selaginella schizobasis Bak., J. Bot. 21: 333. 1883. *S. tuerckheimii* Hieron. ex Donn.-Sm., Enumeratio Plantarum Guatemala 6: 67. 1903, *nom. nud.*

Prostrate or decumbent, on forest floor or in thickets or wooded ravines sea level to 1,000 m; Alta Verapaz; Chimaltenango; Izabal; Petén; Suchitepéquez. Southern Mexico; British Honduras; Honduras; Nicaragua; Costa Rica.

Plants terrestrial, heterophyllous throughout; stems prostrate or decumbent, branched throughout, articulate, sometimes prolonged and flagelliform at apex; rhizophores produced from the upper surface of the stem for much of its length, or occasionally throughout; lateral leaves 2.5–4 mm long, narrowly oblong to elliptic-lanceolate, acute or subacute, the margins subtinture to serrulate (sometimes ciliolate toward base and then the cilia 0.1 mm or less), subcordate to (mostly) sagittate at base, with at least one of the basal lobes acute, straight, and touching or overlapping the axis; axillary leaves narrow-elliptic, the margins commonly serrulate, the base biauriculate with auricles conspicuous, divergent and sometimes bearing cilia 0.2 mm long or less; median leaves 1.5–2.5 mm long, obliquely ovate-acuminate or short-aristate, the margins entire to serrulate, peltate, i.e., a single, rounded, lobelike projection extending below the point of attachment, this ca. $\frac{1}{3}$ – $\frac{1}{4}$ the length of the leaf; strobili 4–20 mm long, slightly to strongly tetragonous, bearing a single megasporangium at base; sporophylls 1–2 mm long, acute or acuminate, slightly to sharply carinate; megaspores light tan or gray, with strongly pronounced, white, reticulate ridges; microspores tawny.

This and *S. sertata* are sometimes difficult to separate, especially when comparing the younger branches. However, the older lateral and axillary leaves of *S. schizobasis* commonly have rather conspicuous basal lobes or auricles, as described in the key. In Alston's key to the North American heterophyllous species, *S. sertata* is separated solely on the basis of the flagelliform apices of the main stems, but this is not a consistent character. Occasionally, plants have fully expanded apices, just as a few plants of *S. schizobasis* have greatly elongated, flagelliform apices. Axillary leaves of *S. sertata* are commonly eciliate, although occasionally, cilia may be found at or near the base, and then are only 0.1 mm long or less. The spreading basal auricles of *S. schizobasis* are almost always short-ciliolate,

the cilia usually 0.1–0.2 mm long. In an unpublished dissertation (1978) from the University of Tennessee (Knoxville, Tennessee), Paul Somers, Jr., maintains that *S. schizobasis* is merely an ecotype of *S. sertata*.

Selaginella sertata Spring, Mem. Acad. Roy. Sci. Belgique 24: 104. 1850. *S. nicaraguensis* Bak., J. Bot. 21: 333. 1883.

Prostrate, on forest floor, 150–400 m; Santa Rosa; Sololá. Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama.

Plants terrestrial, heterophyllous throughout; stems prostrate, branched throughout, articulate, commonly greatly prolonged and flagelliform at apex; rhizophores springing from the upper surface of the stem for much of its length, or throughout; lateral leaves 2–4 mm long, narrowly oblong to elliptic-lanceolate, acute or subacute, the margins entire to serrulate (sometimes ciliate toward base and then the cilia 0.1 mm or less), rounded or truncate at base, lacking basal lobes or auricles; axillary leaves narrow-elliptic or lanceolate, the margins subentire to serrulate, or short-ciliate at base (cilia 0.1 mm or less), the base rounded or truncate, lobes or auricles essentially lacking; median leaves 1.5–2.5 mm long, obliquely ovate-acuminate or short-aristate, the margins entire to serrulate, peltate, i.e., a single, lobelike projection extending below the point of attachment, this ca. $\frac{1}{3}$ the length of the leaf; strobili 4–12 mm long, slightly to strongly tetragonous, bearing a single megasporangium at base; sporophylls 1–2 mm long, acute or acuminate, somewhat to sharply carinate; megaspores beige, with strongly pronounced white, reticulate ridges; microspores tawny.

This and *S. schizobasis* are very closely related and are often confused. See treatment of the latter for further discussion.

Selaginella silvestris Aspl., Ark. Bot. 20A, 7: 30. 1926.

Prostrate to suberect, in wet forests or thickets or wooded ravines, on forest floor or sometimes on rocks, sea level to 2,500 m; Alta Verapaz; Escuintla; Izabal; Quezaltenango; El Quiché; San Marcos; Suchitepéquez; Zacapa. Southern Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama; Colombia; Ecuador; Peru; Bolivia.

Plants terrestrial, or occasionally epipetric, heterophyllous throughout; stems prostrate to suberect, branched throughout, articulate; rhizophores present at base of stem or along $\frac{2}{3}$ its length, produced from the upper surface of the stem; lateral leaves 3–4 mm long, obliquely oblong or elliptic, obtuse to subacute, the margins entire to serrulate, broadly rounded to subcordate at base, not or scarcely auriculate; axillary leaves elliptic or oblong-elliptic, the margins entire, the base exauriculate; median leaves 1.5–2.5 mm long, elliptic to obovate, short-aristate, the margins entire to serrulate, biauriculate at base, the auricles unequal or subequal, small and inconspicuous; strobili 3–10 mm long, strongly to scarcely tetragonous, bearing a single megasporangium at base; sporophylls 1–2 mm long (megasporophylls somewhat larger), acuminate to aristate, scarcely to sharply carinate; megaspores beige, gray or off-white, with strongly pronounced, white, reticulate ridges; microspores tawny or beige.

This perhaps is most closely related to *S. kunzeana* A. Br. of South America, southern Central America, and Mexico. Whereas the auricles of the median leaves in *S. silvestris* are small, inconspicuous, and usually subequal in length, those of *S. kunzeana* are very unequal, one of them being quite large and conspicuous. Also, *S. kunzeana* has narrower axillary leaves, and the awns of median leaves are much more pronounced.

Selaginella stenophylla A. Br., Index Sem. Hort. Bot. Berol. App: 22. 1857. *S. incurvata* Bak., J. Bot. 21: 99. 1883. *S. miradorensis* Hieron., Hedwigia 43: 30. 1904.

In forests or clearings, on clay banks of ravines or streams, rarely in rock crevices, 900–1,500 m; Alta Verapaz. Mexico.

Plants terrestrial, rarely epipetric, heterophyllous; stems ascending or suberect, solitary or remote, never caespitose, stramineous, branched nearly from the base; rhizophores borne only in the proximal $\frac{1}{3}$ – $\frac{1}{2}$ of the plant, produced from the lower surface of the stem; lateral leaves 1.8–3 mm long, well spaced on the main stem, approximate to contiguous on the branches, oblong to elliptic-lanceolate, acute, rounded to subcordate at base, the margins subentire to serrulate, rarely with a few ciliolae at very base; axillary leaves lanceolate, subacute, rounded to subcordate at base, the margins serrulate to setulose; median leaves 1–2 mm long, ovate to broadly lanceolate, long-acuminate to (more commonly) short-aristate, irregularly cordate at base, at least those of the stem and main branches with 1–2 free, conspicuous lobes or auricles, the margins setulose or setose; strobili 3–12 mm long, somewhat to strongly tetraginous; sporophylls acute, to 1.5 mm long, somewhat to sharply carinate; megaspores white, gray, or beige; microspores bright orange.

Selaginella steyermarkii Alston, Ann. Mag. Nat. Hist., ser. 12, 7: 638. 1954.

Prostrate, creeping on rocks or cliffs, or on rocky hillsides, 1,000–2,300 m; Baja Verapaz; Huehuetenango (type from near San Sebastián, altitude 2,000–2,200 m, *Steyermark 50501*); Quezaltenango; El Quiché; Sololá; Zacapa; occasionally found in other departamentos, cultivated in gardens. Southern Mexico. *Doradilla* (fide Steyermark, Huehuetenango).

Plants epipetric, homophyllous, the leaves borne on all sides of the stem and branches; rhizomes and stolons absent; stems long, prostrate, producing rhizophores nearly to the apex; vegetative leaves 2–3 mm long, appressed for most of their length, in age becoming pale brown to tawny or reddish, linear-lanceolate to linear-deltoid, abruptly adnate at base, acuminate at apex and commonly tipped with a whitish seta, the margins abundantly ciliate; strobilus tetraginous, radially symmetrical, with sporophylls in 4 ranks; sporophylls convexo-concave, abaxially rounded to angular or sometimes slightly carinate, deltoid or deltoid-ovate, acuminate and often tipped with a whitish seta, the margins denticulate to short-ciliate (at least above the base); megaspores pale orange to yellow, microspores bright orange.

Apparently this is the only homophyllous species occurring in Guatemala, so it cannot be confused with any other. Of the homophyllous species, it is one of a few with leaves becoming reddish in age.

Selaginella tarapotensis Baker, J. Bot. 21: 98. 1883. *S. faucium* Liebm. ex Baker, tom. cit. 333 (not Liebm. ex Fourn. 1872, nom. nud.).

In forests or wooded ravines, on clay banks or on the forest floor, 940–1,600 m; Alta Verapaz; Baja Verapaz. Southern Mexico; Panama; Colombia; Ecuador; Peru; Bolivia.

Plants terrestrial, heterophyllous throughout; stems stramineous or pale greenish, prostrate, approximate to remote, never caespitose, branching from base nearly to apex; rhizophores borne throughout and produced from lower surface of stem; lateral leaves 2–3.5 mm long (at least in plants of Mexico and Central America), well spaced on the main stem, approximate to contiguous on the branches, spreading from the axes at 70°–90° angles, often lustrous and silvery beneath, obliquely lanceolate or oblong-lanceolate, obtuse or subacute, inequilateral at base, broadly rounded acroscopically, cuneate basiscopically, margins entire (or rarely serrulate at base acroscopically); axillary leaves lanceolate or narrow-ovate, subequilateral at base, otherwise like the lateral leaves; median leaves 1–2.5 mm long (including the apical awn), ovate to elliptic, long-aristate, the midvein strongly raised and prominent throughout, terminating in a conspicuous awn which is $\frac{1}{2}$, to equalling, the length of the lamina, margins entire or minutely serrulate, obliquely and scarcely subcordate at base; strobili 3–15 mm long, strongly tetraginous, especially before

maturity; sporophylls 1–1.5 mm long, carinate, usually spreading at maturity; megaspores white; microspores pale orange.

This and *S. faucium* were described at the same time by Baker and were said to differ principally in size of plants and width of branches. The Peruvian *S. tarapotensis* is a smaller, more delicate plant, with branches about 3 mm broad. The Mexican *S. faucium* is much larger and coarser, with larger branches 4 to 6 mm broad. Alston (1955) combined the two, and rightly so, for other than size and texture, there are no significant differences. The coarser plants are found in southern Mexico and Guatemala. Other than one or two specimens, the South American plants are the delicate variants represented by the type.

Selaginella umbrosa Lemaire ex Hieron., in Engl. & Prantl, Die Natürlichen Pflanzenfamilien 1(4): 683. 1901. *S. lemairei* Hieron., Hedwigia 58: 287. 1917, *nom. provis.* *S. erythropus* var. *major* Spring, Mém Acad. Roy. Sci. Belgique 24: 156. 1850.

In forests, thickets or wooded ravines, on banks of lakes or streams, rarely on bases of trees or on rocky slopes, sea level to 650 m; Alta Verapaz; Izabal; Petén; San Marcos. British Honduras; Honduras; Costa Rica; Panama; Jamaica; Grenada; Barbados; Tobago; Colombia; Venezuela; Brazil; Peru.

Plants commonly terrestrial, erect, heterophyllous, but homophyllous as to the stem below the leafy portion; stems solitary or remote, never caespitose, unbranched in the proximal $\frac{1}{3}$ – $\frac{2}{3}$, deep reddish nearly throughout; rhizophores few, basal, produced from the lower surface of the stem; lateral leaves 1–3 mm long, older ones turning reddish, approximate to contiguous, or slightly imbricate on the branches, obliquely ovate or lanceolate, falcate, acute, margins essentially entire, but ciliate in the proximal half, at base broadly rounded acroscopically, truncate to geniculate basiscopically; axillary leaves ovate to broadly lanceolate, acute, rounded at base, the margins entire to serrulate, but ciliate in the proximal portion; median leaves 0.7–2.7 mm long, oblique-ovate, acute or (occasionally) acuminate, subcordate at base or unequally biauriculate, the margin entire to remotely serrulate or setose, but with 3–4 cilia at base; strobili to ca. 1 cm long, sharply tetragonous; sporophylls ca. 1 mm long, sharply carinate; megaspores white; microspores bright orange.

This is similar in most respects to the South American *S. haematodes* (Kze.) Spring. In fact, the two are often confused where their ranges overlap in Panama. The most obvious difference is in the lateral leaves, with those of *S. umbrosa* rather conspicuously ciliate in the proximal portion and sharply truncate or geniculate at base basiscopically. Lateral leaves of *S. haematodes* are essentially naked along the margin and are rounded at the base.

ISOETACEAE

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Plants heterosporous, small, herbaceous, perennial, aquatic, amphibious, or terrestrial; corms subterranean or epiterranean, rounded or elongated horizontally or vertically, 2- to many-lobed, the lobes often difficult to discern; roots numerous, dichotomously branched, produced within a single or several root grooves (fossae) which are continuous along the basal or lateral surfaces of the corm or are confined to a single side of the corm (as in older specimens of *I. andicola* [Amstutz] Gomez); leaves quill-like, (2–) 5–40 (–128), imbricate,

spiral or rarely distichous, erect to recurved, with an expanded, winglike margin, triangular or rounded in cross section, with a single, unbranched midvein, surrounded by 4 transversely septate air channels and 0–6 or more peripheral groups of fibrous supporting cells; stomata numerous to lacking; ligule small, delicate, broadly to narrowly triangular, ephemeral, arising from a pit on the adaxial leaf surface just above the sporangium, frequently with a fleshy labium inserted between the ligule and sporangium which partially or completely covers the ligular pit; sporangia adaxial, borne singly at or near the base of the leaf, covered by or partially covered by the membranaceous velum; megaspores globose-tetrahedral, 200–800 (–1,000) μm in diameter, variously ornamented, developing into endosporic gametophytes which produce several archegonia; microspores ellipsoid, 20–60 μm long, variously ornamented, developing into endosporic gametophytes which produce but a single antheridium.

This is a monotypic family containing the single, cosmopolitan genus *Isoetes*, with 175–200 species. A second genus, *Stylites*, from Peru and Bolivia, has often been recognized and considered distinct based on its unusual corm morphology, root production, and sporangial position. These characters, while unusual, are not, however, sufficiently discrete to merit generic distinction. The unusual vertically elongated corm of *Stylites* appears to be nothing more than an adaptation to a cushion-plant habitat where the surrounding substrate is continually and rapidly increasing. The unusual root production in adult plants of *Stylites*, where roots are produced only at the apex of the single, laterally positioned fossa is likewise a modification to this unusual habitat, and young plants have been found in which the fossa is continuous around the base of the corm and extends up each side. Finally, other taxa in the genus *Isoetes* (e.g., *I. andina* Spruce ex Hook.) have sporangia located fairly high up on the adaxial leaf surface.

ISOETES Linnaeus

REFERENCE: N. E. Pfeiffer, Monograph of the Isoetaceae, Ann. Missouri Bot. Gard. 9: 79–233. 1922.

Characters are those of the family.

The "quillwort" genus, *Isoetes*, can be mistaken for no other group of ferns or fern allies; but species are often difficult to delineate, even with the aid of a compound microscope. The problems are greater still in the study of dried specimens. Most of the so-called "diagnostic" characters used in the past are inconsistent and/or misunderstood. Pfeiffer (1922) and others attempted to base a classification partially on such features as shape and size of the ligule, number of corm lobes, presence or absence of stomata, and number of fibrous peripheral bundles. Most of these are difficult to assess, especially in dried specimens, and the nature of many such characters is dependent upon the age of the plant or leaf or the habitat (whether the plant is fully submersed, partially so, or completely terrestrial).

To add to the taxonomic difficulties, there is the problem of paucity of specimens, especially in more remote areas of the Tropics. Plants are easily overlooked, or are passed over by collectors as clumps of sedges or rushes. Additional efforts to seek out these plants must be made, especially in the Tropics, but more intelligent collecting and data recording are necessary as well. Attempts to collect plants within a particular habitat should include individuals of varying degrees of maturity, as well as those from the center and at the periphery of the colony, and those of varying degrees of submersion. Furthermore, individual plants should be tagged to record these three pieces of data.

Isoetes occurs along fresh or tidal shores, in or at margins of lakes, ponds, and streams, in ditches and wet meadows, alpine bogs, and rarely in low forests or rocky slopes. Aquatic taxa are frequently evergreen, whereas terrestrial species often lose all their leaves and can remain dormant for one or several years. Two species have been collected in Guatemala, and a third, from British Honduras, perhaps to be expected in Guatemala.

- a. Megaspores bacillate, the projections much taller than broad, and evenly distributed on the proximal and distal surfaces. *I. panamensis*.
- a. Megaspores smooth, verrucate or pustulate, the protuberances as tall as or shorter than broad.
 - b. Megaspores pustulate, the protuberances smooth, rounded, distinct on both proximal and distal surfaces, evenly distributed and well developed, even near the equatorial ridge. *I. cubana*.
 - b. Megaspores smooth or verrucate, the protuberances when present poorly developed and then rounded or well developed and then apically muricate, the protuberances becoming smaller and less distinct near the equatorial ridge. *I. montezumae*.

***Isoetes cubana* Engelm. ex Baker, J. Bot. 18: 110. 1880.**

Thus far known only from the type location in Cuba and two locations in British Honduras.

Corm rounded, 3(?)-lobed, 0.4–2 cm in diameter; fossa continuous around corm; leaves 10–40, these 10–46 cm long, 0.5–1.75 mm broad at mid-length, triangular in cross section, with 3 darker, shallow, lateral ridges continuing to the apex; differentiated leaf border chartaceous, brown to barely transparent, 1–2 mm broad at the sporangium, gradually tapering into the leaf 1.5–6 cm above the base; sporangia elliptic, 5–9 mm long, 3–4 mm broad, tan, unspotted; velum incomplete, 0.3–0.6 mm broad along the lateral edges of the sporangium, 0.6–0.7 mm deep along the upper edge of the sporangium; ligule not apparent, eroding to below the labium; labium transversely ovate, 0.4–1.2 mm high, 1.1–3 mm broad, tan, margins entire to laciniate; megaspores white or gray, 270–470 (\bar{x} = 351) μ m in diameter, pustulate, with 20–50 or more projections on the distal surface, each of these 30–70 μ m in diameter, as high as or shorter than broad, occasionally merging laterally to form short, meandriform markings, equatorial and proximal ridges straight, thick and prominent; microspores gray, 25–35 (\bar{x} = 29) μ m long, 20–30 (\bar{x} = 23) μ m wide, exospore 1–4 μ m thick, sparsely to densely echinate (smooth in immature spores).

This species is apparently aquatic or semiaquatic, based on label data, the flexuous nature of the leaves in the British Honduras material, and the dense covering of diatoms on the leaves of the Cuban collections. Although the British Honduras material does not possess aborted scalelike leaves, this may be an artifact of collecting, and more specimens need to be examined before this character can be fully assessed.

The British Honduras and Cuban material is very close morphologically, but does differ in some of the megaspore and microspore characters. The megaspore pustules in the British Honduras material are generally more numerous, more crowded, and tend to be somewhat shallower than those in the Cuban material. In the latter, there are fewer than 40 pustules on the distal surface, while in the former, there are generally more than 50. Although the microspores of the Cuban material cannot be completely characterized due to their immature nature, it is obvious from measurements of the most mature spores found that they are somewhat longer (\bar{x} = 30 μ m) than those from British Honduras (\bar{x} = 28 μ m) and less densely ornamented.

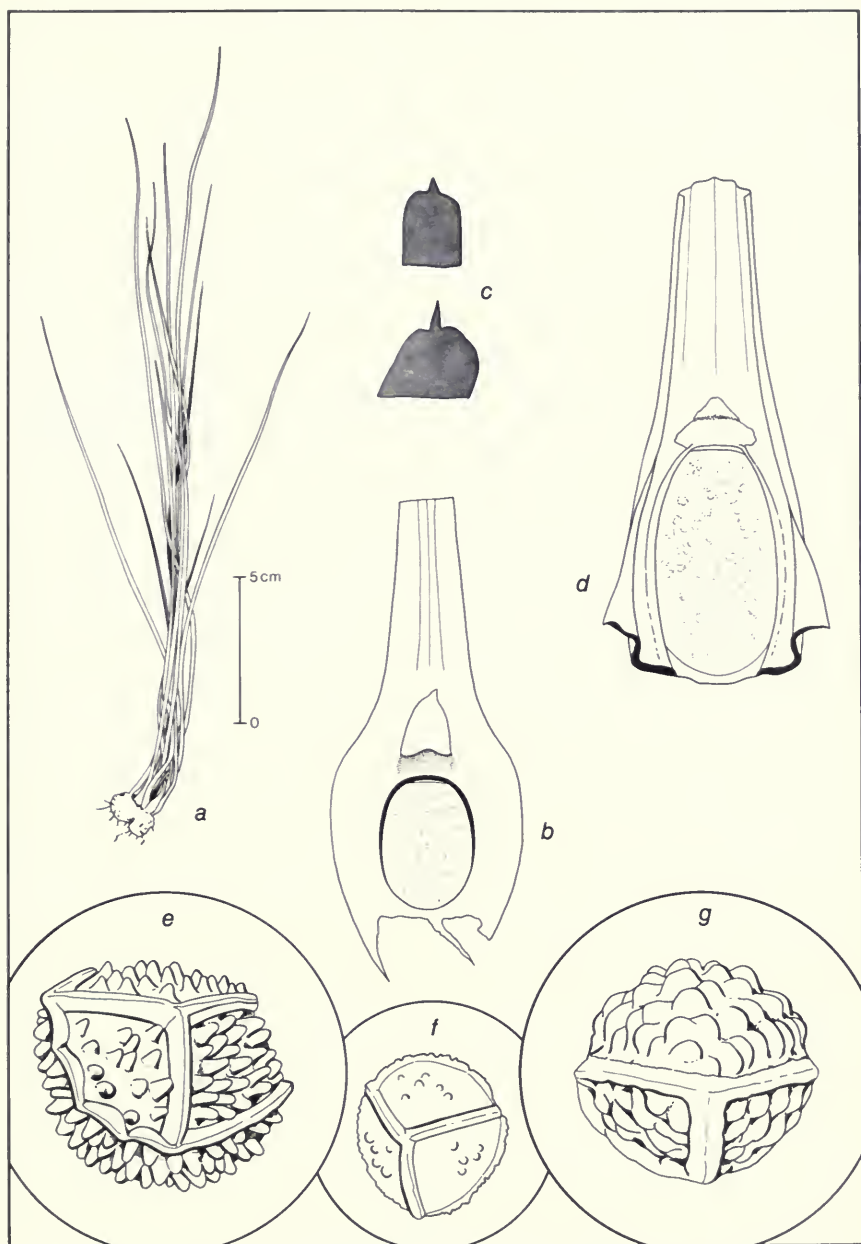


FIG. 10. *Isoetes*. a–c, *I. montezumae*: a, habit, $\times \frac{1}{2}$; b, leaf base, $\times 6$; c, scale leaves, $\times 5$. d–e, *I. panamensis*: d, leaf base, $\times 5$; e, megaspore, $\times 94$. f, *I. montezumae*, megaspore, $\times 38$. g, *I. cubana*, megaspore, $\times 110$.

Isoetes montezumae A. A. Eaton, Fern Bull. 5: 25. 1897.

In shallow ponds, wet depressions, and meadows, 2,000–3,500 m; Huehuetenango; San Marcos. Mexico (type from the state of Mexico: damp soil, plains near Flor de María, Aug. 28, 1890, *Pringle* 3459).

Corm rounded to slightly elongated laterally, 2-lobed; fossa continuous around the corm; leaves 7–21, these 4–23 cm long, 0.4–1.3 mm broad at mid-length, stiff, upright to slightly recurved, triangular in cross section with 3 green, inconspicuous lateral ridges continuing upward to near the apex, leaf tip abruptly tapering to a blunt, rounded apex, differentiated leaf border chartaceous, light brown, nearly transparent, 0.4–2 mm broad at the sporangium, gradually tapering into the leaf 1.5–4.5 mm above the base; scale leaves persistent, black to dark brown, oblong to transversely oblong, 2–2.5 mm long, 2–4 mm broad, with mucronate apex, 0.5–1 mm long; sporangia elliptic to circular, 2.5–4.5 mm long, 2–3.5 mm broad, tan, lightly spotted to unspotted; velum absent, or incomplete, 0.2–0.3 mm broad along the upper edge of the sporangium; ligule occasionally represented by a tan, triangular to ovate remnant, 1–1.25 mm long, 1–1.6 mm broad; labium very small, barely covering the ligular pit, 0.2–0.3 mm high, 0.6–0.8 mm broad, tan, entire; megaspores white, not shiny, 350–660 (\bar{x} = 510) μ m in diameter, smooth to inconspicuously pustulate, the protuberances smaller and more crowded near the equatorial ridges, each protuberance 20–30 μ m high, 20–30 μ m broad, equatorial and proximal ridges straight, distinct; microspores light gray, 34–45 (\bar{x} = 39) μ m long, 27.5–35 (\bar{x} = 31) μ m broad, exospore 3.25 μ m thick, minutely granular, often with larger tubercles superimposed on the granular surface.

Isoetes montezumae is found throughout central and southern Mexico from Jalisco and Mexico to Oaxaca and Chiapas. Its southern limit appears to be in central Guatemala, though it should be expected in Honduras and El Salvador. The plant is quite seasonal, as evidenced by its habitat and the persistent scale leaves which apparently protect the apical meristem during drought conditions.

The description given above is based primarily on Guatemalan material. This material differs, however, in several respects from the more typical Mexican collections. In general, the Guatemalan plants are much smaller, have fewer leaves, and have much smaller sporangia. The megaspore ornamentation is also much less well developed. Typically, *I. montezumae* has distinct tubercles on both proximal and distal surfaces, though, like the Guatemalan material, there is a tendency to show numerous but less well-developed protuberances near the equatorial ridge. However, even within Mexico, there is a tremendous amount of variation in many of these characters, and it seems reasonable at this time to assign the Guatemalan collections to *I. montezumae*.

Isoetes panamensis Maxon & Morton, Ann. Missouri Bot. Gard. 26: 272. 1939. *I. pacifica* Svenson, Amer. Fern J. 34: 123. 1944. (type from Ecuador, Prov. Guayas, south of Engabao, Chanduy Hills, Mar. 22/23, 1941, *Svenson* 11002.)

In seasonal rain pools, boggy swamps, and depressions, 950–1,500 m. As yet, this species is known only from two localities in Guatemala: Chiquimula and Jutiapa, and from one locality each in Costa Rica, Panama (type from Prov. Panama, vicinity of Bejuco, Aug. 7, 1938, *Woodson, Allen & Seibert* 1685), Ecuador, and Peru.

Corm rounded, 3-lobed, 0.7–3 cm in diameter; fossa continuous around corm; leaves 9–128, these 17–28 cm long, 0.5–2 mm broad at mid-length, stiff, upright, triangular in cross section, with three, darker, shallow, lateral ridges continuing to the apex; persistent scale leaves not present, leaf tip finely tapering to a thin, pointed apex, stomates present, differentiated leaf border chartaceous, tan, nearly transparent, 2–4 mm broad at the spo-

rangium, gradually tapering into the leaf 3.5–10 cm above the base; sporangia obovate, 13 mm long, 5–7 mm broad, tan, unspotted; velum virtually absent, 0.2–0.5 mm broad along the lateral edges of the sporangium, absent along the upper edge of the sporangium; ligule usually absent, occasionally represented by a blackened, triangular fragment, 3–4 mm high, 4–4.5 mm broad, its base partially or completely covered by the labium; labium transversely elliptic, 1–2 mm high, 4.5 mm broad, whitened, margins laciniate; megaspores white, 350–580 (\bar{x} = 451) μ m in diameter, bacillate, the projections up to 70 μ m in height, ca. 35 μ m in diameter; equatorial ridge thin, often undulate, proximal ridges thin, distinct; microspores ash-gray, 27–40 (\bar{x} = 34) μ m long, 20–33 (\bar{x} = 26) μ m broad, exospore ca. 2.5 μ m thick, smooth to sparsely echinate.

Isoetes panamensis grows near sea level from Peru to Costa Rica. According to Svenson (1944), the Ecuador material was collected in pools which are dry for part of the year; such habitats are probably common throughout the range of this species, though label data is scanty. The spotty distribution of the species will undoubtedly be filled in as more intensive collections are made along the west coasts of Central America and northern South America.

The type descriptions of *I. panamensis* and *I. pacifica* coincide in most characters. The greater leaf width reported for *I. panamensis* is most likely a reflection of the more vigorous nature of this collection, which may be a result of lower water stress in that locality. The only significant discrepancy in the two descriptions is in the reports of microspore "diameter." Maxon and Morton report a diameter of 25 μ m for *I. panamensis*, whereas Svenson gives a size range of 36–40 μ m for the microspores of *I. pacifica*. Given the fact that the spores are ellipsoid, it is possible that Svenson's measurements were of microspore length, while those of Maxon and Morton were of width. Recent measurements of spores from both types indicate that the spores are quite comparable in both length and width.

Recently, L. D. Gómez has described a new species, *I. savannarum*, from Costa Rica, which strongly resembles *I. panamensis*. The descriptions of these two plants are sufficiently similar to warrant a close examination of the two before relationships can be postulated.

COMPREHENSIVE INDEX TO PARTS I, II, AND III

This index covers all three parts of the pteridophyte flora of Guatemala which have appeared in *Fieldiana: Botany* and consists of 719 pages and numerous plates. The numbers following an entry refer first to the part number of the flora and second to the page(s) where the entry occurs.

The index includes all accepted names (in roman), synonyms (*italics*), common English names (roman), and vernacular names (*italics*). Entries (in roman) are also included for medicinal or local uses. Hyphenated words and multiple words are alphabetized letter by letter. Names of persons, when considered useful to the reader, also have been indexed. Page numbers of descriptions are in **boldface**; page numbers of illustrations are in *italics*.

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